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Structural Features and Phylogenetic Relationships Among Larvae of Genera of Gyrophaenine Staphylinids (Coleoptera: Staphylinidae: Aleocharinae)

James S. Ashe

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James S. Ashe

Department of Zoology
Field Museum of Natural History
Chicago, Illinois 60605-2496

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Structural Features and Phylogenetic Relationships Among Larvae of Genera of Gyrophaenine Staphylinids (Coleoptera: Staphylinidae: Aleocharinae)

Abstract

Systematics, structure, and phylogenetic relationships of known larvae of genera of the aleocharine tribe Gyrophaenina were investigated. Larvae representing 6 of 13 described genera, including all Holarctic genera, except *Brachida* Kr. and *Encephalus* Kr., were available for study. A great variety of structural features, especially in detailed variations in chaetotaxy, mouthpart structure, and characteristics of the tergal gland and associated structures of abdominal segment VIII, were found to be useful for systematic and phylogenetic comparisons among genera. Distribution and variation of these structural characteristics among gyrophaenine larvae and immatures of other aleocharines are discussed. Larvae of all available genera of the Gyrophaenina are described and characterized, a key is provided for separation, and illustrations of structural features of representative late instar larvae of all available genera are provided.

Based on an analysis of transformation series of 34 larval characters, a cladistic analysis of available genera was developed. The Gyrophaenina is shown to be monophyletic, based on 17 derived larval characteristics. Sister group relationships among genera are congruent with most branches of a previously published cladogram of all gyrophaenine genera, based on adult characteristics. Though presently unresolvable discrepancies in phylogenetic relationships of some genera remain, these do not require revision or rejection of previously developed conclusions of classification or evolution of gyrophaenines based on cladistic analysis of adult features. Comparisons of cladograms based on the independent character systems of larvae and adults provide a very robust test of previously developed cladograms and subsequent conclusions based on them.

Introduction

Immatures of the large and diverse staphylinid subfamily Aleocharinae are commonly encountered in a variety of microhabitats. For many of these, their abundance suggests that they may have a significant impact on community structure. However, very little is actually known about the habits of aleocharine larvae, and, indeed, it is rarely possible to identify even the most commonly encountered individuals to tribe or genus, much less to species. A part of this difficulty stems from the great diversity of taxa included in the subfamily Aleocharinae, a group that Arnett (1968) described as the "poorest known section of the entire order Coleoptera" (p. 283). Because of the difficulty of confidently identifying adults of this large and inadequately known group and the fact that a diversity of adults are often found together with larvae in many habitats, accurate association of larvae with adults is commonly impossible and even identification of reared material is sometimes questionable.

In addition to the typical taxonomic problems encountered in studying aleocharine larvae, a further limitation to studies of immatures has been the lack of a consistent reference framework within which to compare structural features among superficially similar larvae. This has resulted in many sketchy and inconsistent descriptions of aleocharine larvae which cannot provide unambiguous dis-

crimination among larvae of most taxa. Recent development of the requisite comparative system for examination and discussion of chaetotaxic features of aleocharine larvae (Ashe & Watrous, 1984) represents the first attempt to develop such a comprehensive base for study.

Ashe (1984) recently stabilized the generic classification of the subtribe Gyrophaenina and provided a detailed cladistic analysis and discussion of structural, behavioral, and ecological features of its members. He noted that gyrophaenines are exceptional in that they are obligate inhabitants of fresh mushrooms as both larvae and adults. Within this habitat they feed exclusively on the active spore-producing layer (the hymenium) of fresh mushrooms. This is a highly unusual habit among aleocharines, most of which are thought to be predators. This specialized habit and the consequently very limited generic diversity of aleocharines found on fresh mushrooms (a considerably greater diversity of predaceous aleocharines is attracted to mushrooms past their prime) improves the possibility of making confident larval-adult associations as well as providing for development of relatively easy and effective rearing techniques (Ashe, 1981). Gyrophaenines, therefore, offer excellent opportunities for the study of structural and behavioral features of closely related higher taxa within the Aleocharinae.

Despite this, very few gyrophaenine larvae have been described. Fewer still have been described in the detail required for comparative study among taxa. The only comparative study of gyrophaenine larvae available is that of White (1977), who studied larvae of several British species of *Gyrophaena* and *Agaricochara*. However, the limited taxonomic range of larvae available to him, possible incorrect associations, and the inadequate reference base available for study of aleocharine larvae at that time resulted in several taxonomic conclusions which cannot be supported after examination of a greater diversity of taxa (see below).

Other gyrophaenine larvae are known only from descriptions of individual species of *Gyrophaena* (Rey, 1886; Boving & Craighead, 1930; Paulian, 1941) or *Phanerota* (Ashe, 1981). Description of the larva of *Gyrophaena manca* Erichson (Heeger, 1853) is not that of a gyrophaenine (White, 1977; Ashe, 1984).

Other published comparative studies of aleocharine larvae are also uncommon. The only detailed study of taxa within a single tribe of aleocharines known to me is that of athetine aleocharines by Topp (1975). This paper clearly illustrates the diversity of characteristics in chaetotaxy, antennal structure, and other features which are available for systematic analysis within a single, structurally relatively homogenous, tribe. However, there is no certainty that the species and higher taxa included in Topp's study are closely related within the diverse and taxonomically very difficult Athetini. This seriously limits subsequent attempts to determine the phylogenetic and taxonomic implications of the variation noted.

This investigation of gyrophaenine larvae represents the first known to me that attempts to compare all known larvae of a demonstrably monophyletic group within the Aleocharinae.

The general purpose of this paper is to provide the basis for identification and additional study of larvae of genera of the subtribe Gyrophaenina and to enlarge the systematic and phylogenetic framework developed by Ashe (1984), based primarily on studies of adults, for study of this particularly interesting group of staphylinids. In addition, since the chaetotaxic system developed by Ashe and Watrous (1984) is relatively new and has not been used previously as a basis for the comparative study of aleocharine larvae, this study will serve as demonstration of use and as an initial test of the effectiveness of this system. Finally, no attempt to study the phylogenetic implications of character systems of aleocharine larvae has been made previously. Therefore, this investigation will provide an initial discussion of pertinent character systems of gyrophaenine larvae and compare the resultant hypotheses of phylogenetic relationships of genera based on these larval characteristics for congruence with those developed by Ashe (1984) based on adult features.

I hope that this study will encourage similar comparative studies of other groups of aleocharine larvae.

Materials and Methods

Materials

Gyrophaenine immatures used in this study were obtained and identified both by association with adults based on collecting and by a variety of rearing techniques. Gyrophaenine larvae and adults can often be collected together on the host fungus, especially on intermediate aged, fleshy gilled mushrooms. It is, however, often difficult to establish the identity of late instar larvae found on

older fleshy mushrooms without rearing them because adults have commonly already abandoned these older mushrooms for fresher fruiting bodies. This is particularly a problem because, in many instances, adults of several species of gyrophaenines may visit a single mushroom, though all may not breed there. This differs considerably from the situation on woody polypore mushrooms. The number of species found on these mushrooms is much fewer, and usually only a single species of gyrophaenine is found on a given mushroom. In addition, adults and larvae of all instars are often found together on mature fruiting bodies.

Because of the possibility that larvae found on a mushroom may not represent the same species as adults collected in association, great care must be exercised in establishing species identifications based on such associations. However, after a few firm associations of larvae with adults are known, it becomes possible to make much more confident larval-adult associations by providing limits to the possibilities. Also, experience with the local gyrophaenine fauna provides for development of information about host ranges of local species, thereby making identifications based on associations much more confident.

Rearing provides much more reliable larval identifications. Ashe (1981, 1984) discussed techniques for rearing larvae of gyrophaenines. Generally, most gyrophaenine larvae can be easily reared by maintaining them together with the mushroom on which they were found until they mature. Ashe (1981) found that placing the mushroom in an inverted (gills up) position on moist paper towels was suitable. However, I have since found that maintenance of mushrooms in petri dishes with 0.5 to 1.0 cm of plaster of Paris in the bottom is more effective. It is much easier to maintain the proper moisture on plaster than with paper towels. This is especially important because if the mushrooms become too wet they will often rot before larvae complete development. However, it is not difficult to maintain larvae and adults of most gyrophaenine species under such conditions as long as mushrooms are available. In addition, adults confined with the proper host mushroom will often lay eggs which can be reared for larval association. Some gyrophaenines live on mushrooms that produce toxic volatiles when confined in a closed container, which kill any animals living on them. I have not been successful in keeping specimens of these species in the laboratory.

Larvae which are ready for pupation become restless and leave the host mushroom. In those instances when larvae were reared to adults, these mature larvae were either transferred to a soil-peat mixture for pupation or pupation substrate was pressed into one corner of the petri dish. In this latter circumstance, pupation usually occurred in the soil-peat mixture, and fewer larvae were damaged by unnecessary handling.

Based on the above methods for obtaining identified larvae and in consideration of the problems encountered in making accurate larval-adult associations noted above, I have established several criteria for determining identity of larvae. The designation of identification criteria used in the descriptive sections of this paper is indicated in parentheses.

1) Association (assoc.)—Larvae are found in association with numerous (>10 to 15) adults of a single species on either a single mushroom or a closely associated group of fruiting bodies of the same species. Larvae are not considered firmly associated if two or more species of adults are found together with them, even if individuals of one species predominate.

2) Larvae from eggs associated with adults (ex ovo)—Eggs found associated with adults of a single species are reared to mature larvae. This is similar to associated larvae, but identifications are more firmly established because early collection decreases the possibility that adults which produced larvae have already left the mushroom, leaving behind, or perhaps being replaced by, adults which are not conspecific with associated larvae.

3) Reared (reared)—Larvae or eggs found associated with a single species of adult are reared to maturity, and randomly selected larvae are reared to adults. Identification is considered established if all reared adults are conspecific with the original associated adults.

Borrowed material cannot be justified under these criteria because detailed conditions of collection are not available. Therefore, borrowed material labeled "associated" is assumed to have larvae determinations established under criterion 1 above, provided no other information suggests that this assumption is not valid.

Preparation and Examination of Material

Examination of the wide variety of structural features available for comparative study of aleocharine larvae requires that material be properly prepared and examined with adequate equipment. I have found that examination of cleared larvae

on permanent slides with compound optics is particularly useful. Proper clearing of soft parts of the larva is especially important. In this study, larvae which were preserved in alcohol for one or more years were first cleared for 10 to 30 minutes in cold, concentrated potassium hydroxide (KOH) and then transferred through a wash of distilled water to Nesbitt's solution for 10 to 30 minutes. This results in larvae in which the soft parts are exceptionally clear but in which cuticular structural features are not cleared to transparency. Larvae cleared in this way provide excellent slide mounts with cuticular features clearly visible and minimally distorted by preparation procedures. Those larvae which have been preserved in alcohol for extended periods (10 or more years) do not clear well and must be left much longer in both KOH and Nesbitt's. However, extended periods in either of these solutions will cause considerable damage to cuticular structures: wrinkling of cuticle, curling and deformity of setae, loss of setae, overclearing, etc. Therefore, larvae treated in this way must be watched carefully. The most effective clearing is achieved by placing freshly killed larvae directly into Nesbitt's solution for 10 to 30 minutes, depending on size and initial transparency.

For examination, I mounted cleared larvae directly from Nesbitt's solution onto permanent microscope slides into Hoyer's mounting medium. Before adding the cover slip, larvae were properly arranged in the mounting medium, and mouthparts were teased open by applying gentle pressure basoventrally on the head capsule with a pair of fine forceps. Slides were dried in a drying oven for 3 to 4 weeks and then ringed with glyptol to prevent development of the air channels characteristic of slides mounted with Hoyer's medium.

Primary examination of mounted larvae was done with a Wild M-20 compound microscope or a Leitz Dialux 20 defraction interference compound microscope at magnifications of 200 to 1,000 times. Drawings were made with the aid of a drawing tube. Selected representative larvae of each genus were critical point dried, gold coated, and examined with a Cambridge S-4 scanning electron microscope.

Materials and Taxa Included

The subtribe Gyrophaenina is currently composed of 13 described genera (Ashe, 1984). Of these, representatives of six genera, including all Holarctic genera except *Brachida* and *Encephalus*, are available as confidently determined immatures. For a variety of reasons, including rarity, exotic ranges of taxa, and others, availability of reliably determined larvae of other gyrophaenine genera cannot be expected in the foreseeable future. Therefore, generic revision of immatures of the subtribe Gyrophaenina is considered timely despite incomplete coverage.

Generic descriptions herein are based on late instar larvae of all species of the genus examined. For all genera except *Brachychara* Sharp, larvae of the type species were available, and these were used as an initial basis for the descriptions. Larvae of other species of the genus were compared with these, and the descriptions appropriately modified. In addition, immatures of the type species were used to provide illustrations of distinctive features whenever possible.

All materials examined are in the collection of the Field Museum of Natural History, except those generously on loan to me from the British Museum (Natural History) (BMNH) or the Museum of Comparative Zoology (MCZ).

The variety of larvae of identified taxa of the subtribe Gyrophaenina examined in the course of this study should provide a reasonable sample of the structural diversity of most higher taxa of gyrophaenines. However, the sample is necessarily limited when compared with the total diversity of the subtribe. It therefore seems possible that characterizations of immatures of each of these genera may require modification as larvae of other species become available for study. I especially hope that this study will provide a basis in systematics of gyrophaenine larvae that will encourage additional investigation of immatures, life history and habits, and ecology of these beetles.

Natural History and Development

All members of the Gyrophaenina for which natural history information is available are obligate inhabitants of fresh mushrooms as both larvae and adults. Within the mushroom habitat they feed exclusively on the spore-producing layer, the hymenium, from which they graze maturing spores, basidia, and other hyphal structures. This characteristic habitat and feeding mode departs markedly from the predacious habits of most aleocharines, including the variety of other staphylinids which visit fresh mushrooms. The habit of feeding only on the hymenium layer also differs signifi-

cantly from that of most other mushroom-inhabiting insects, most of which feed on the flesh of the cap, stem, or gills, primarily by burrowing into the mushroom.

Many of the structural, developmental, and life history features of gyrophaenines reflect both this unusual way of using the mushroom resource and the distinctive features of the mushroom habitat. The most striking structural adaptation to the gyrophaenine mode of mushroom habitation is in structural characteristics of the maxilla. Structure of this mouthpart appears to be functionally important in the grazing feeding mode used by these beetles. In both adults and larval gyrophaenines the maxilla is modified to form an apical brush of numerous closely spaced spines (see Ashe, 1984, for a detailed discussion of structural and functional characteristics). In adults, these spinose patches are on the lacinia of the maxilla, while they form the surface of the mala of larvae. These spinose structures are found only among gyrophaenines, as far as is known, and are very unlike features of any other aleocharine. Similarity among these structures in adult and larval gyrophaenines, in contrast to the distinctly different maxillae of adults and immatures of most aleocharines, is striking and suggests similar functional requirements for the gyrophaenine feeding mode throughout the life cycle.

Known features of the natural history of gyrophaenines have been discussed by Ashe (1984). Within the variety of mushroom-producing fungi, gyrophaenines live primarily on very ephemeral fleshy gilled mushrooms (Agaricales) or more persistent polypore mushrooms (Polyporaceae). Different lineages within the subtribe specialize in each of these mushroom types. The two groups of mushrooms offer different habitat characteristics to beetles which live on them. They differ in a number of general characteristics, including persistence, place of spore production (and subsequent availability of the hymenium layer), and duration of spore production. These differences potentially have a profound effect on variation in population structure, life cycle, and development of gyrophaenines.

Members of most *Gyrophaena* and *Phanerota* are found only on more ephemeral fleshy gilled mushrooms. It seems reasonable that these gyrophaenines are under the most severe time restraints on development and life cycle. Since both adults and larvae live between the gills and feed exclusively on the active hymenium layer, they can occupy only fresh mushrooms. Often fleshy gilled mushrooms are suitable habitats for only a few days to a week. This then represents the maximum time available for adult feeding, mating, oviposition, eclosion, and maturation of larvae, all of which take place on the same mushroom. Consequently, the life cycle is remarkably compressed. Ashe (1981) found that eggs of *Phanerota fasciata* (Say) were laid on the gills soon after adults were attracted to very young fruiting bodies. Eggs hatched within 24 hours, and there were three larval instars. Instar I lasted an average of 14.2 hours, instar II 14.8 hours, and instar III about 2 days. Development from hatching to fully mature larvae, ready to leave the mushroom for pupation, required 3.2 days at room temperature. Reared larvae of *Gyrophaena* used in this study had very similar developmental times. Pupation occurred within a silken pupal cell constructed in the intertices of soil or leaf litter and lasted 4 to 14 days for available reared species. These very short developmental times appear to be a direct response to the ephemeral nature of gilled mushrooms.

In contrast, members of *Agaricomorpha, Brachychara, Agaricochara,* and some *Eumicrota* are found only on more persistent, woody or leathery, polypore mushrooms. Fruiting bodies of these mushrooms may be present for a month or more. Unfortunately, general features of the life history of those gyrophaenines which live on polypores are much more inadequately known. No species which occupies these mushrooms has been reared, and other detailed observations are lacking. However, the greater longevity of polypore mushrooms and consequently, the relatively more extended time of active spore production suggests that these beetles are not under the severe time restraints on development of those that live on gilled mushrooms. As a result, they may have somewhat less rapid developmental times or other features of the life cycle may be more leisurely. However, this supposition has yet to be confirmed.

These extremes of habitat features of general types of mushrooms occupied by gyrophaenines are joined by a range of more or less persistent gilled mushrooms and more or less ephemeral polypore mushrooms. These mushrooms have their own distinctive gyrophaenine fauna comprised principally of a few species of *Gyrophaena* and most *Eumicrota.*

It is particularly interesting that members of gyrophaenine lineages which specialize on one of these mushroom types are seldom or never found on fruiting bodies with significantly different habitat characteristics. This suggests that features of

the life cycle, structure, or physiology limit the range of habitats among available mushrooms which are usable by members of a gyrophaenine species.

Interpretation of Setal Patterns

The general system used for discussion of development and distribution of setae and associated structures in this study is that of Ashe and Watrous (1984), and nomenclature and abbreviations are consistent with those used in their study. Chaetotaxic characteristics are very stable at a variety of taxonomic levels, and distribution of setae, their relative positions, and their relative development provide numerous characters for description and phylogenetic analysis. The chaetotaxic system developed by Ashe and Watrous (1984) provides a framework within which these patterns can be examined and discussed.

The relatively reduced chaetotaxy of gyrophaenine larvae, with extensive loss of typical setae and sensilla, creates numerous problems in determining homology of setae. This problem primarily results from the use by Ashe and Watrous (1984) of characteristic setae and sensilla as reference points for determining homologies of associated chaetotaxic structures. It becomes much more difficult to do this confidently when many setae and sensilla are absent and others are potentially in unexpected positions. Therefore, misinterpretation and possible inaccuracies in assigning and naming homologous setae may result both from the relatively reduced chaetotaxy of gyrophaenines as well as from the very incomplete knowledge of chaetotaxy of other aleocharine larvae as a whole. However, with this perspective in mind, initial studies of larval chaetotaxy are required that use an internally consistent system to provide the basis for critique and discussion of both the overall pattern of setal structures of aleocharine larvae and the system itself.

This section is intended to clearly describe my reasoning in establishing names and homologies for setal structures on gyrophaenine larvae and to provide the basis for review and possible subsequent modification.

Loss of setae and sensilla from the head of gyrophaenine larvae (figs. 1, 46) has resulted in particularly severe problems in interpretation of cranial chaetotaxy. All frontal setae recognized by Ashe and Watrous (1984) are present and can be easily homologized; however, the frontal region lacks campaniform sensillae. In the epicranial region, the dorsal row (Ed1–3) is complete with three setae. The two setae immediately dorsal to the ocellus are interpreted to represent the lateral row (E1). The most anterior of these setae is interpretated as El1 even though it is posterior to campaniform sensilla Ec1 rather than anterior to it as indicated by Ashe and Watrous (1984). This implies that the position of either the seta or sensilla has shifted. If this interpretation is correct, then seta El3 is absent. All four posterior setae (P1–4) of the epicranial region are present and allow interpretation of the associated campaniform sensilla present in some gyrophaenines as Ec3. The seta immediately posterior to the ocellus represents the first seta of the marginal row (Em1). The two posterior setae of the marginal row (Em2–3) are absent. The two small to very small setae immediately below or below and slightly behind the ocellus are interpreted to represent the complete temporal row (T1–2), though these are slightly more anterior and ventral in most gyrophaenine larvae than similar setae of *Atheta coriaria* Kr. (Ashe & Watrous, 1984). However, in specimens of *Gyrophaena nana* Payk., these setae are posterior to the ocellus. The three most anterior and ventral cranial setae of larval gyrophaenines represent the setae of the lateral row (L1–3). In most, the most anterior seta of this row (L1) is anterior and ventral to the ocellus and is significantly larger than other setae in the lateral row of most gyrophaenine larvae, though L1 is dorsal and slightly posterior to L2 in larvae of *Agaricochara laevicollis* Kr. In all gyrophaenine larvae examined, all campaniform sensilla of the lateral cranial region and all ventral setae and ventral campaniform sensilla are absent.

Chaetotaxy of legs of gyrophaenine larvae is typical of that described for larvae of other aleocharines by Ashe and Watrous (1984), though differences in relative size and robustness of setae are apparent among larvae of different genera.

Chaetotaxy of thoracic and abdominal terga are also significantly reduced from the more generalized pattern described in athetine larvae by Ashe and Watrous (1984). On the pronotum, setae of the anterior, lateral, and posterior rows can be clearly homologized by referring to the characteristically larger and more prominent setae of A2, A4, L4, P2, and P4. These peripheral rows of setae are complete with five setae in each row (fig. 9) or, in some gyrophaenine larvae, two setae are absent in the lateral row anterior to the very prominent lateral seta L4 (fig. 55). The two lateral setae

which are missing in these latter larvae are here interpreted to be L2 and L3. If this assignment is correct, L1 is placed somewhat more posteriorly on the pronotum of most larvae in which L2 and L3 are absent than on those which have the lateral rows complete. This interpretation is supported by the absence of L2 and L3 from the pronotum of all first instar gyrophaenine larvae and most other first instar aleocharine larvae.

Campaniform sensilla are represented on the pronotum of late instar gyrophaenine larvae only by C1, C3, and C6. These can be easily recognized by their characteristic positions in relation to distinctive reference setae.

Discal setae of the pronotum of gyrophaenine larvae examined are represented only by two setae on each side of the midline in most, a medial and a lateral seta. Complete lack of other reference setae and campaniform sensilla in the discal region of the pronotum make it very difficult to determine the true homologies of these two setae. For purposes of this study these medial and lateral discal setae are interpreted to represent Da2 and Dc2, respectively (fig. 9). A third more lateral seta on the mesonotum, metanotum, and abdominal terga of larvae of *Agaricochara* is similarly interpreted to represent Dd2 (fig. 10). There are several reasons for these designations. (1) These setae are in characteristic positions in relation to setae of posterior and lateral rows, respectively, which are occupied by similar setae in larvae with more complete discal setae (see Ashe & Watrous, 1984). (2) This interpretation is consistent with the presence of the meical transverse set (Da2–Dd2) of most first instar aleocharine larvae. (3) It is consistent with the serially homologous positions of these two setae on more posterior segments. (4) This interpretation does not conflict with presence of a serially new seta (interpreted as Db3 in accordance with Ashe & Watrous [1984]) in the posterior row of abdominal terga I–VII. It is recognized that interpretation of these discal setae in Da2, Dc2, and Dd2 may prove to be incorrect when aleocharine larvae become better known; however, at present, no other interpretation seems reasonable.

Discal setae Da2 and Dc2 of the pronotum are interpreted as serially homologous with discal setae in similar positions on more posterior terga. In larvae of those gyrophaenines in which Da2 is positioned in the posterior row of abdominal terga I–VII (figs. 26, 41), determination of which posterior seta represents Da2 is facilitated by referring to campaniform sensilla C6 and posterior seta P2 as markers.

The posterior row of abdominal terga I–VII has an additional seta in the space between P3 and P4 which is not found on thoracic terga (fig. 11). This seta is very tentatively interpreted as homologous to that seta designated Db3 of athetine larvae by Ashe and Watrous (1984). However, lack of any serially homologous seta on thoracic terga of gyrophaenine larvae makes this interpretation uncertain. It may subsequently prove better to designate this seta as of new origin (i.e., not homologous to any of the characteristic discal setae), though no presently available evidence suggests this.

The chaetotaxic pattern of tergum VIII is markedly affected by prolongation of the posteromedial margin in association with the very well-developed tergal gland of gyrophaenine larvae (figs. 59, 60). If the two large setae of the posterior margin are homologous with P2 and P4 and Ashe and Watrous (1984) are correct in their interpretation that the seta on each side of the posteromedial lobe is a new addition (Pa1), then the campaniform sensilla near the base of the lobe is C6, P3 is absent, and Db3 is displaced anteriorly from its normal position in the posterior row on more anterior abdominal terga. Ashe and Watrous (1984) interpreted the brushlike seta in the posteromedial lobe of gyrophaenine larvae as homologous to P1 of tergum VIII of other aleocharine larvae, an interpretation that is followed here. Associated with posteromedial elongation of the tergum, Da2 and Dc2 form an oblique row, with Dc2 far anterior to Da2.

Identification and Description

Late Instar Larvae of the Subtribe Gyrophaenina

DIAGNOSIS—Among aleocharine larvae, immatures of the Gyrophaenina can be recognized by the obliquely truncate mala of the maxilla with numerous more or less closely spaced teeth or spines (fig. 7) and an emarginate scale at the distal apex (figs. 101–102); the broad, only slightly protruded ligula; spinose sensory appendage of antennomere 2; distinctive reduced chaetotaxy of head (figs. 1, 46), thoracic terga (figs. 9–10, 55), and abdominal terga (figs. 11, 57), particularly presence of only discal setae Da2 and Dc2 and campaniform sensilla C1, C3, and C6 on the pronotum (fig. 9); markedly developed posteromedial protuberance of abdominal tergum VIII

associated with a well-developed tergal gland; tergal gland reservoir large with internal ringlike sclerotized supports and four sclerotized, singly to doubly looped to more or less straight tubular gland ducts (fig. 59); absence of hooks on the pseudopod (fig. 15); and association with fresh mushrooms.

DESCRIPTION—**General**—Length of mature larva, 1.1–4.2 mm. General body form elongate, slightly flattened, or robust and broadly oval in cross section, broadest at mesonotum and intermediate abdominal segments. Color of mature larva whitish to very light grayish brown dorsally, with or without apical abdominal segments darker. Microsculpture absent except for scattered micropoints on one or more sclerites of abdominal segments III–X in some. Vestiture of long simple setae.

Head—Length to width ratio various, range 0.72–1.1. Ocellus single on each side, small, inconspicuous (fig. 1) to relatively large and prominent (fig. 82). Ecdysial sutures distinct and complete to antennal fossae, or indistinct and not attaining antennal fossae. Epicranial gland opening present, distinctly developed. Setation reduced, E13, Em2-3, V11-3, and V1 absent. Campaniform sensilla with only Ec1 and, in some, Ec3 present. Antenna 3 articled, relative lengths of articles various; sensory appendage of antennomere 2 spinelike, tapered uniformly from base to more or less acute apex, about 1.0–2.0 times length of constricted portion of antennomere 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 present or absent, very small when present, IIS2 spinose, similar in size to IIS1 (fig. 3) or smaller (fig. 18) or reduced to very small spinule (fig. 33), IIS1 broadly rounded apically in most, less than ¾ times length of sensory appendage; antennomere 3 with three apical solenidea (IIIS1–3) and one subapical solenidea (IIIS4), solenidea not noticeably inflated or modified. Labrum as in Figure 5, not divided posterolaterally into additional sclerotized areas; setation with Ld1 and Ld2 setose but smaller than other labral setae, setae not modified to spinose or peglike structures. Epipharynx with anteromedial concentration of sensory pores and densely pubescent area on each side of midline; distribution of sensory elements and patches distinctive (figs. 21, 50). Mandibles elongate, slender, more or less acute apically, with single preapical tooth; right and left more or less similar; adoral surface simple, without serrations; laterally with two small setae in basal half (fig. 2) or more distal seta markedly reduced (fig. 47) and one campaniform near basal seta insertion. Maxilla as in Figures 7, 37, and 72; cardo large, more or less transverse, incompletely divided medially by sclerotized ridge; stipes elongate, more or less of uniform width throughout; mala not delimited by desclerotized region; mala more or less obliquely truncate, with surface more or less densely covered with numerous spines, spines small and very densely arranged (fig. 22) or larger and less densely arranged (fig. 73); apical termination with emarginate foliose scale (fig. 101); other spinose or bladelike scales present ventrolaterally (fig. 38) or not (fig. 74); adoral surface of mala flattened, with (fig. 74) or without (fig. 53) scattered spinules laterobasally; maxillary palpus of three palpomeres in addition to incomplete basal palpifer, length of palpomeres various, article 3 with digitiform sensory peg basally. Adoral surface of labium with or without inwardly directed setose processes. Labium as in Figures 4, 34, and 49; sclerites consisting of prementum and fused mentum and submental sclerites; ligula short and broad, broadly rounded or truncate apically, slightly (fig. 34) or moderately (fig. 69) or not (fig. 85) emarginate medially; labial palps 2 articled, article 1 0.3–0.5 times length of 2, article 2 with apical spine large (fig. 19) or very small (fig. 69).

Thorax—Pronotum (fig. 9) slightly sclerotized, ecdysial suture distinct or slightly developed; setation reduced, discal rows represented only by Da2 and Dc2, lateral rows complete or L2 and L3 absent, accessory setae absent; campaniform sensilla reduced, C2, C4, and C5 absent. Mesonotum (fig. 10) with anterior border slightly sclerotized, ecdysial suture distinct or slightly developed; setation similar to pronotum except anterior row present in slightly sclerotized anterior portion of sclerite and reduced to spinose sockets, lateral setae L2, L3, and, in some, L5 absent, discal setae Da2 and Dc2 present, of similar size (fig. 10), or Dc2 markedly larger (fig. 40), Dd2 present or absent (in most). Metanotum similar to mesonotum. Legs typical of subtribe, slender and elongate (fig. 42) or shorter and more robust (fig. 54).

Abdomen—Abdominal terga I–VII markedly transverse, anterior margin slightly sclerotized, pretergal gland well developed; setation with Da2, Db3, and Dc2 present, Db3 in posterior row of setae between P3 and P4, Da2 discal (fig. 10) or in posterior row lateral to (fig. 41) or mesal to (fig. 26) campaniform sensilla C6; lateral seta L1 present (fig. 11) or absent (fig. 57). Posterior margin of abdominal tergum VIII markedly produced as a broad lobe; tergal gland reservoir large, well developed, sclerotized with ringlike thickenings for

support; ducts of tergal glands present as four sclerotized tubes, tubes with a single loop (fig. 59) or second loop slightly developed to complete (fig. 13) or loop obsolete (fig. 95); setation with seta P1 present as modified spatulate (fig. 30) or brushlike (fig. 44) seta, posterior setae P3 and P5 absent. Urogomphi 1 articled, 0.3–0.6 times length of abdominal segment IX. Tergum X more or less short, length of sclerotized portion less than total width. Pseudopod slightly developed, without sclerotized hooks.

Identification

NOTES ON THE KEY—Most of the characteristics used for separation of taxa in this key have not been previously used in keys for identification of aleocharine larvae. Therefore, they have not been tested for general reliability. Though characters used here are suitable for separation of the gyrophaenine larvae at hand, other characters may prove more useful or reliable after additional taxa and specimens have been compared. Under these circumstances, the key to late instar larvae of the genera of the Gyrophaenina provided here should be considered provisional.

Many of the structural features used as major key characters are small and/or difficult to see unless material is properly prepared and examined. For most specimens, suitable slide mounts of larvae (see Methods above) must be examined by using compound optics.

Larvae of *Gyrophaena, Phanerota,* and *Eumicrota* are difficult to separate in a key. This is a result both of the general similarity of larvae of these genera and of the great structural and taxonomic diversity included in the genus *Gyrophaena.* As a result, and in consideration of the diversity of taxa of *Gyrophaena* which are not known as larvae, couplets 4 and 5 may not accurately identify all larvae of the genera encountered. If this proves to be true, the key will require modification.

The key provided here is intended to be artificial in that it has been developed solely for the purposes of reliable identification. Similarities between the key and hypothesized cladistic relationships among genera are a coincidental result of the usefulness of phylogenetically meaningful features for identification.

Key to Known Late Instar Larvae of Genera of the Subtribe Gyrophaenina

1.(2) Pronotal lateral setae L2 and L3 present (fig. 9); epicranial campaniform Ec3 present (fig. 1); ligula slightly (fig. 4), moderately (fig. 34), or deeply emarginate (fig. 19); ligula with (figs. 19, 34) or without (fig. 4) large, conspicuous setose sensilla on each side of midline; mala moderately (fig. 7) to very densely (fig. 37) spinose, with distal spines only slightly (fig. 37) to moderately (fig. 7) larger than proximal spines; apicolateral surface of mala with moderately (fig. 8) to well-developed (fig. 38) accessory spines, ribbon-like and/or spatulate scales 2

1′. Pronotal lateral setae L2 and L3 absent (fig. 55); epicranial campaniform Ec3 absent (fig. 46); ligula moderately (fig. 69), slightly, or not (fig. 49) emarginate; ligula without large, conspicuous setose sensilla on each side of midline (fig. 69); mala slightly (fig. 73) to moderately (fig. 52) spinose, with distal spines markedly larger than proximal spines (fig. 73); apicolateral surface of mala with accessory scales not developed into elongate spines, ribbon-like and/or spatulate scales (fig. 74) 4

2.(1) Head as long or longer than broad (1.0–1.1 times as long as broad) (fig. 1); ligula with small spinose sensilla on each side of midline (fig. 4); mesonotum with discal seta Dd2 present (fig. 10); discal seta Da2 of abdominal terga I–VII not in posterior row (fig. 11); posterior seta P1 of abdominal tergum VIII spatulate, only slightly brushlike, apex finely serrate, serrations incised 0.05–0.07 times length of seta (fig. 14) ..... *Agaricochara* Kr.

2′. Head moderately (fig. 31) to slightly (fig. 16) transverse (0.7–0.9 times as long as broad); ligula with large, conspicuous setose sensilla on each side of midline (figs. 19, 34); mesonotum with discal seta Dd2 absent (fig. 25); discal seta Da2 of abdominal tergum I–VII in posterior row (figs. 26, 41); posterior seta P1 of abdominal tergum VIII spatulate, only slightly brushlike (fig. 30), or broad and very brushlike (fig. 44) 3

3.(2) Larva more or less robust, broadly oval in cross section; mala with distinct raised area of small

teeth in distal 0.2 (fig. 37); labium with seta at base of labial palpus very large (fig. 34); discal seta Dc2 of mesonotum markedly larger (3.0–4.0 times) than Da2 (fig. 40); discal seta Da2 of abdominal terga I–VII in posterior row between C6 and P2 (fig. 41); posterior seta P1 of abdominal tergum VIII very broad, brushlike, apical serrations incised 0.3–0.5 times length of seta (fig. 44); urogomphus short, about 0.3 times length of tergum IX (fig. 45) ..... *Brachychara* Sharp

3'. Larva more or less dorsoventrally flattened, not robust or broadly oval in cross section; mala without raised area of small teeth in distal 0.2 (fig. 22); labium with seta at base of labial palpus only moderately developed (fig. 19); discal seta Dc2 of mesonotum only slightly larger (1.5–1.7 times) than Da2 (fig. 25); discal seta Da2 of abdominal tergum I–VII in posterior row between P1 and C6 (fig. 26); posterior seta P1 of abdominal tergum VIII spatulate, only slightly brushlike, apical serrations incised less than 0.05 times length of seta (fig. 30); urogomphus longer, 0.6–0.7 times length of tergum IX (fig. 28) ..... *Agaricomorpha* Ashe

4.(1) Bulge of ocellus small to very small (fig. 66); ligula moderately (in most) (fig. 69) to very slightly emarginate; base of adoral surface of mala with small patch of microspinules on each side of midline (fig. 74) ..... *Gyrophaena* Mannerheim

4'. Bulge of ocellus very large (fig. 82) or very small (fig. 46); ligula not at all emarginate (fig. 49); base of adoral surface of mala with broad lobe (fig. 89) or distinct papillate lobe (fig. 53) near insertion of maxillary palpus, without microspinules laterally (fig. 53) or present only near proximolateral border (fig. 89) 5

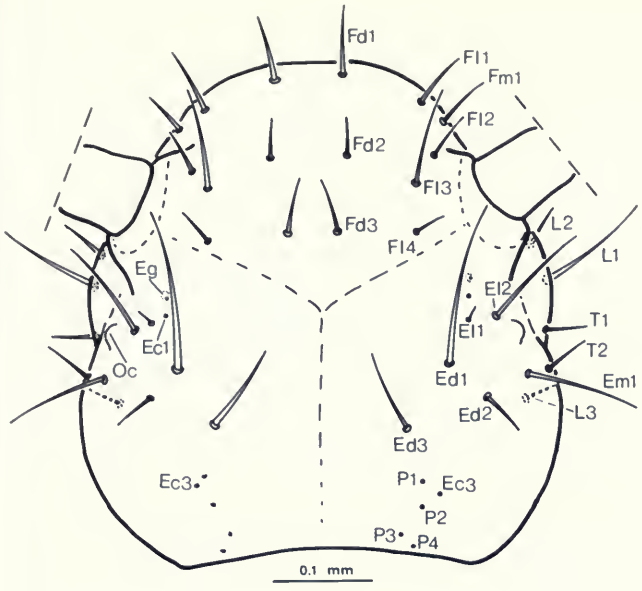
5.(4) Mature larva 2.1–3.5 mm in length; bulge of ocellus very large (fig. 82); loop of abdominal gland ducts obsolete, ducts almost straight (fig. 95); base of mala with microspinules near proximolateral border (fig. 89) ..... *Phanerota* Casey

5'. Mature larvae 1.0–1.7 mm in length; bulge of ocellus small to very small (fig. 46); loop of abdominal tergal gland ducts well developed (fig. 59); base of mala without microspicules (fig. 53) ..... *Eumicrota* Casey

Late Instar Larvae of *Agaricochara* Kraatz (Figures 1-15)

DESCRIPTION—**General**—Length of mature larva 2.1–2.4 mm. General body elongate, slightly flattened, broadest at mesonotum and intermediate abdominal segments. Color of mature larva whitish. Microsculpture absent. Vestiture of long simple setae.

Head (Figure 1)—As long or longer than wide, length to width ratio 1.0–1.1. Ocellus single on each side, small. Ecdysial sutures well developed, lateral arms attaining antennal fossae. Chaetotaxy characteristic of subtribe; campaniform sensilla typical of subtribe, Ec3 present. Antenna as in Figure 3, 3 articled; relative lengths of articles with article 1 1.2 times as wide as long, article 2 2.4 times as long as 1, article 3 0.6 times as long as 2; sensory appendage spinelike, tapered uniformly from base to more or less acute apex, about 2.0 times length of constricted portion of antennomere 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 absent; IIS1 digitiform and rounded at apex, about 0.5 times length of sensory appendage, IIS2 spinose and filiform, 1.0–1.1 times length of IIS1; solenidea of antennomere 3 spinose, pointed apically, not enlarged or inflated. Labrum as in Figure 5; setation with Ld1 and Ld2 of similar size, moderate, not short and stubby. Epipharynx as in Figure 6. Mandibles (fig. 2) with subapical tooth moderately developed, broad lobe in molar region moderately developed; more distal seta of lateral pair present, only slightly smaller than very small proximal seta. Maxilla (fig. 7) typical of subtribe; mala (figs. 7–8) obliquely truncate with 5–6 rows of moderate to very small teeth, teeth slightly larger distally and smaller more proximally; apex of mala with single deeply emarginate foliose scale distally; lateral surface of mala with several toothlike, spatulate and/or foliose scales (fig. 8); base of adoral surface of mala with patch of 4–7 microspinules laterally and 2–3 microspinules adorally in available specimens; maxillary palpus as in Figure 7. Adoral surface of labium (hypopharynx) with numerous, very fine, inwardly and anteriorly directed hairlike processes on each side of midline. Labium as in Figure 4; ligula very short, very slightly protruded, about 0.4–0.5 times length of labial palpus, very broad, truncate, and slightly emarginate medially, apical emargination with slight protruded process medially in some specimens, with small spinose sensilla on each side of



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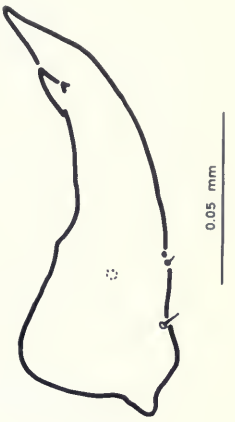

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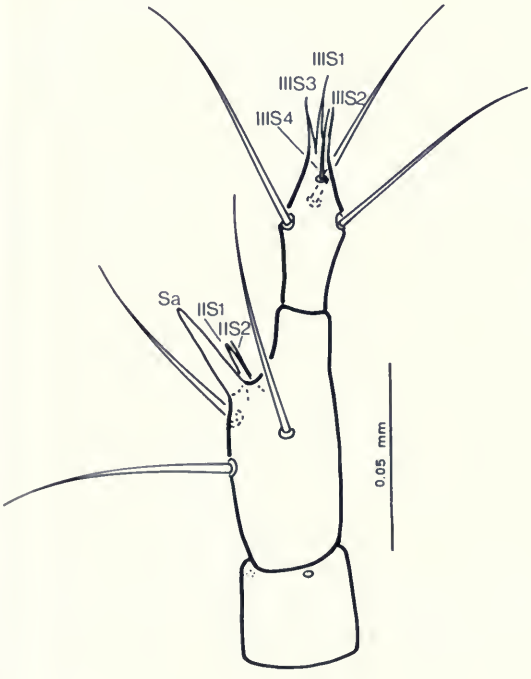

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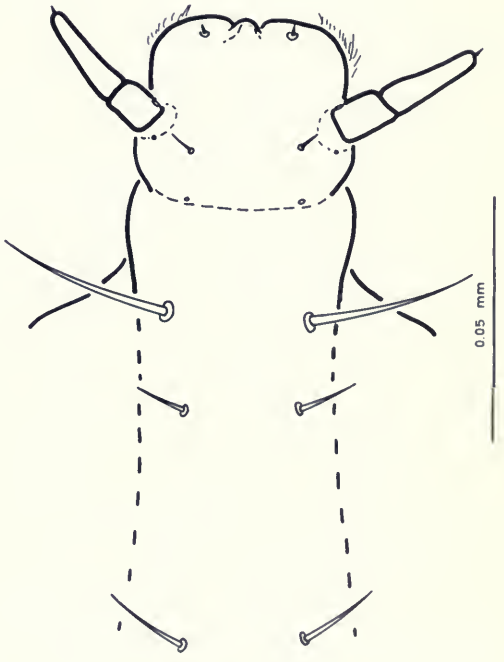

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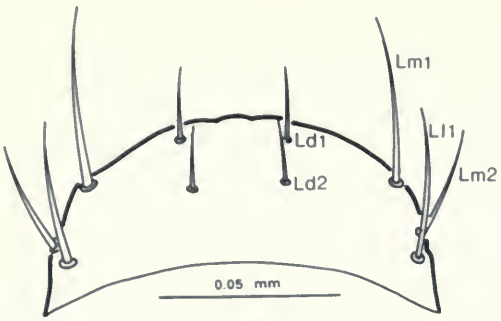
FIGS. 1–4. *Agaricochara laevicollis* Kraatz, larval instar III. **1,** Head, dorsal aspect; **2,** mandible, ventral aspect; **3,** antenna, dorsal aspect; **4,** labium, ventral aspect.



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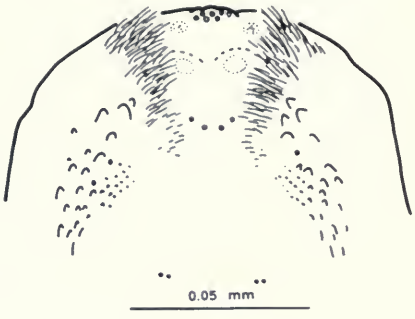

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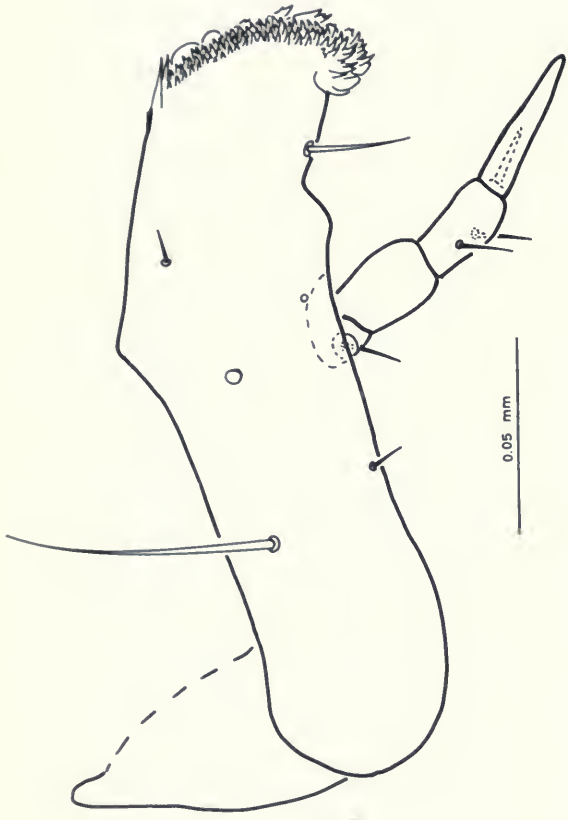

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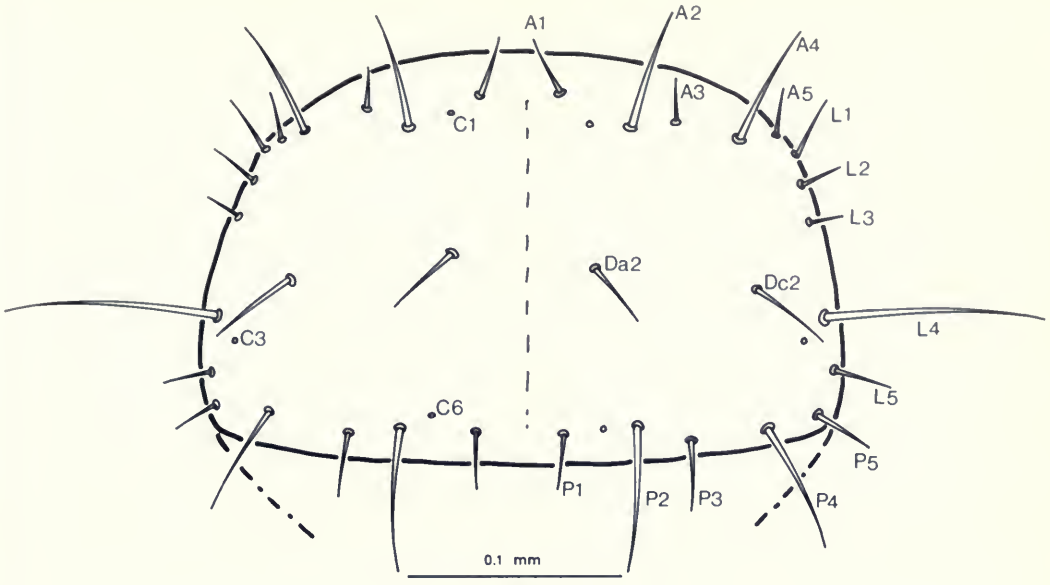
FIGS. 5–8. *Agaricochara laevicollis* Kraatz, larval instar III. **5**, Labrum, dorsal aspect; **6**, labrum, adoral aspect (epipharynx); **7**, maxilla, ventral aspect; **8**, mala of maxilla, dorsal aspect.



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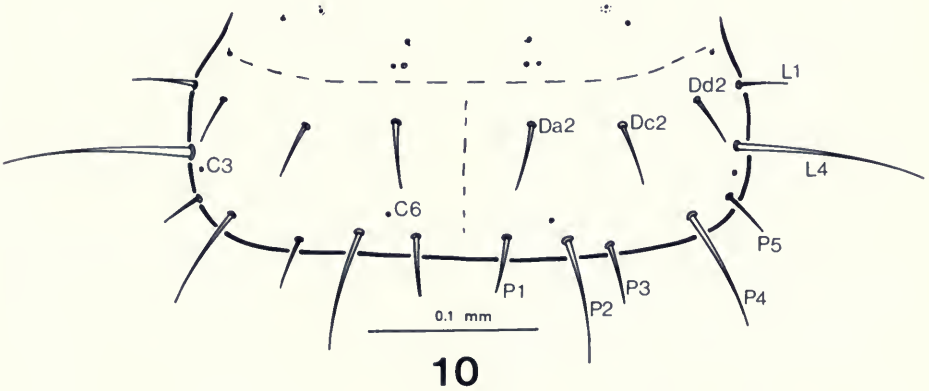

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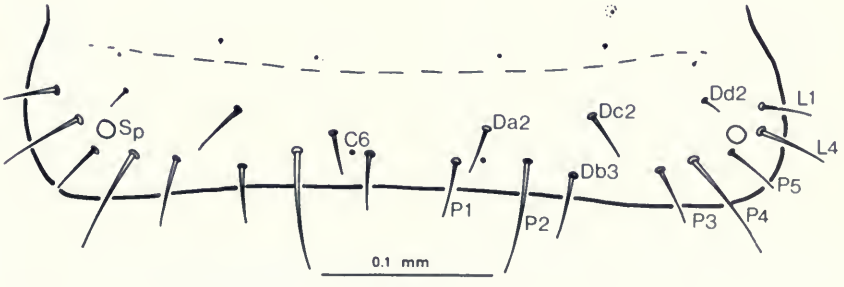

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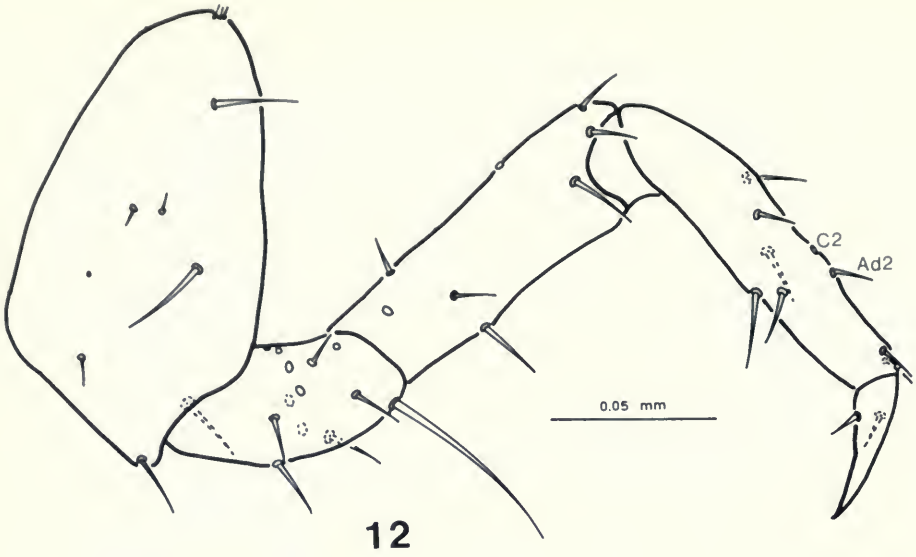
FIGS. 9–11. *Agaricochara laevicollis* Kraatz, larval instar III. **9**, Pronotum; **10**, mesonotum; **11**, abdominal tergum I.



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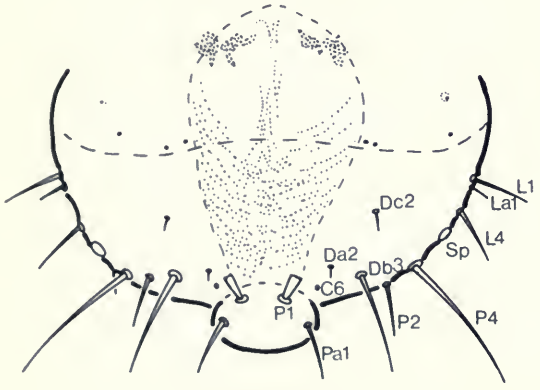

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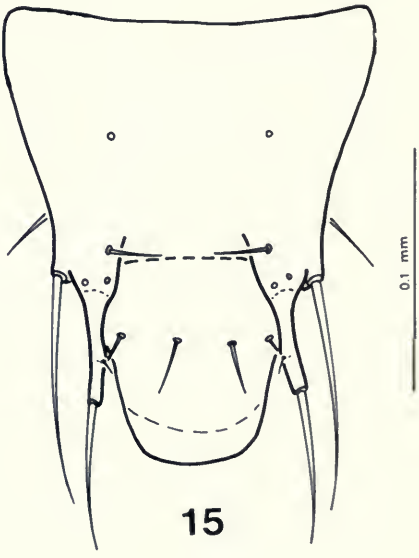

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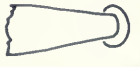

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0.05 mm

FIGS. 12–15. *Agaricochara laevicollis* Kraatz, larval instar III. **12,** Proleg, anterior aspect; **13,** abdominal tergum VIII; **14,** brushlike seta, P1 of abdominal tergum VIII, detail; **15,** abdominal terga IX–X.

midline slightly proximal to apex; labial palpus 2 articled, article 1 about 0.7 times length of article 2, apical spine of article 2 small; seta near insertion of labial palpus moderately developed.

Thorax—Pronotum (fig. 9) only slightly transverse, broadest at base, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 moderately developed, lateral setae L2 and L3 present; ecdysial suture moderately to well developed. Mesonotum (fig. 10) similar to pronotum, except anterior setae reduced to microtrichous pores in slightly sclerotized anterior portion of tergum; discal setae Da2, Dc2, and Dd2 present, moderately developed, Dc2 only slightly longer than Da2; lateral setae L2, L3, and L5 absent. Metanotum similar to mesonotum. Legs as in Figure 12; femur length to width ratio 2.9–3.0.

Abdomen—Abdominal terga I–VII (fig. 11) markedly transverse, anterior margin slightly sclerotized, discal setae Da2, Dc2, and Dd2 present, Da2 not in posterior row, Da2 and Dc2 similar in size, Dd2 very small, Db3 in posterior row mesad to P4. Abdominal tergum VIII (fig. 13) markedly produced posteromedially as a broad, apically subglobose lobe in association with well-developed tergal gland; chaetotaxy as in Figure 13, Da2 and Dc2 present, very small; posterior seta P1 flattened, spatulate and slightly brushlike, apex finely serrate, serrations incised about 0.05–0.07 times length of seta (fig. 14). Tergal gland reservoir distinct, well developed, 1.1–1.3 times length of tergum; gland ducts with single loop well developed and second loop slightly to completely developed. Abdominal tergum IX–X as in Figure 15; urogomphus single articled, about 0.4 times length of tergum.

MATERIAL EXAMINED—*Agaricochara laevicollis* (Kraatz); 4, instar III, assoc.; Welwyn G.C., Ht., 28/1/44, in *P. versicolor,* with *A. laevicollis,* W. O. Steel, 107, used for description, I. M. White (BMNH): *Agaricochara laevicollis* (Kr.); 5, instar III, det. J. S. Ashe; Ash Wyke, Surr., 12.3.45, in woody fungus on oak, E. A. J. Duffy, 4223, F. I. van Emden collection (BMNH).

DISCUSSION—Larvae of the genus *Agaricochara* can be distinguished from those of all other known gyrophaenines by the distinctive quadrate to slightly elongate head and the relatively narrow thoracic segments. They may also be distinguished from larvae of *Brachychara* and *Agaricomorpha* which they resemble in having a complete lateral row of setae of the pronotum (L1–5), epicranial campaniform Ec3 present, and similar features of the mala of the maxilla, by the presence of discal seta Dd2 on the pronotum and discal seta Da2 of abdominal terga I–VII not in posterior row. They further differ from larvae of these two genera by having a pair of spinose sensillae rather than large setiform sensillae on the ligula.

The phylogenetic relationships of *Agaricochara* within the Gyrophaenina are problematic. Characters of larvae available for phylogenetic analysis may be interpreted either as suggesting that *Agaricochara* is sister group to *Agaricomorpha* + *Brachychara* or as indicating that it is sister group to all available gyrophaenine taxa (see Phylogenetic Analysis). Neither of these hypotheses is strongly supported; however, the former is tentatively accepted here. This hypothesis is given additional support if the small spinose sensillae on the ligula of larvae of *Agaricochara* are interpreted as homologous to the setiform sensillae in similar positions on the ligulae of larvae of *Agaricomorpha* and *Brachychara.* In this form the hypothesis is similar to that tentatively accepted by Ashe (1984) based on studies of adults.

White (1977), who based his studies of larvae of *Agaricochara laevicollis* and *Gyrophaena strictula* Er., suggested that *Agaricochara* should include members of the subgenus *Phaenogyra* Scheerpeltz and Höfler of *Gyrophaena.* He based this primarily on the presumed similarities between larvae of these two taxa. I was not able to locate the larvae of *G. strictula* studied by White, though those of *A. laevicollis* used by White "for description" were located at the British Museum (Natural History). Associated larvae of *G. strictula* available to me did not confirm White's findings. Instead, they clearly indicated a relationship of this latter species with *Gyrophaena.* In addition, lack of apotypic features shared by larvae of *Gyrophaena* and related genera and *Agaricochara* and the tentatively accepted hypothesis of a sister group relationship of this latter genus with *Agaricomorpha* and *Brachychara* suggests that *Agaricochara* should not be considered a subgenus of *Gyrophaena* as proposed by White. This provides support for similar findings based on studies of adult characteristics (Ashe, 1984).

Larvae of *Agaricochara laevicollis* have been found on *Polyporus* (=*Coriolus*) *versicolor* and a woody fungus on oak. This confirms the breeding and host association of members of *Agaricochara* with woody or leathery mushrooms, primarily polypores, on logs (see Ashe, 1984).

Late Instar Larvae of *Agaricomorpha* Ashe (Figures 16-30, 99)

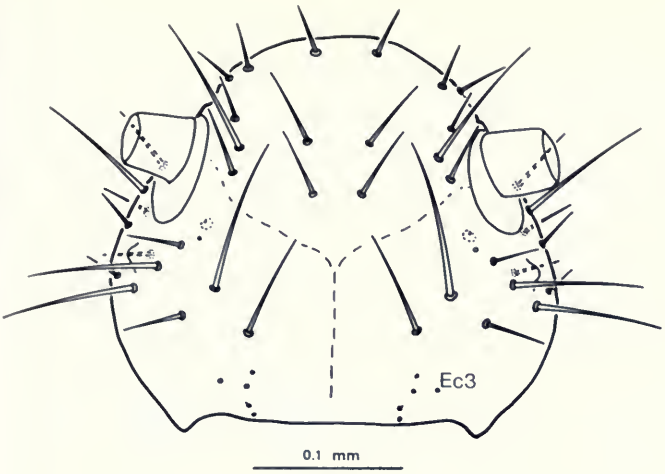
DESCRIPTION—**General**—Length of mature larva 1.7–2.3 mm. General body form elongate, more or less parallel sided, slightly wider at intermediate abdominal segments, slightly dorsoventrally flattened. Color of mature larva whitish with sclerotized portions of terga light gray-brown, abdominal segments VIII–X slightly to moderately darker. Microsculpture absent except for scattered micropoints on terga VI–X, micropoints very loosely organized into slightly developed rows in some specimens.

Head (Figure 16)—Length to width ratio 0.8–0.9. Ocellus single on each side, small, inconspicuous. Ecdysial sutures well developed, lateral arms attaining antennal fossae. Chaetotaxy characteristic of subtribe, campaniform sensilla Ec3 present. Antenna as in Figure 18; 3 articled, relative lengths of antennomeres of specimens of species available, article 1 about as wide as long, 2 2.0 times length of 1, 3 0.7 times length of 2; sensory appendage of antennomere 2 spinelike but slightly rounded apically, 2.0–2.1 times length of constricted portion of antennomere 2; antennomere 2 with solenidea IIS1 and IIS2 present, grouped laterally near base of sensory appendage, IIS3 present, minute, and spinose, IIS1 about 0.6–0.7 times length of sensory appendage, subspinose, tapered but slightly rounded apically, IIS2 spinose, about 0.4–0.5 times length of IIS1; solenidea of antennomere 3 spinose, pointed apically, not enlarged or inflated. Labrum as in Figure 20; chaetotaxy with Ld1 and Ld2 moderately to well developed, setose, not short and stubby, of similar size. Epipharynx as in Figure 21. Mandibles (fig. 17) with subapical tooth moderately well developed; broad lobe in molar area very slightly developed to absent; more distal seta of laterobasal half present as very small microtrichous pore, more proximal seta very small to small. Maxilla (fig. 22) typical of subtribe; mala obliquely truncate with 4–6 rows of small to very small teeth, teeth larger distally but not markedly so; apex of mala with single deeply emarginate foliose scale distally; lateral surface of mala with several toothlike, spatulate, and/or foliose scales (fig. 23), lateral scales less prominent in specimens of some species; base of adoral surface of mala with small patch of microspinules laterally on each side of midline, number and distribution of microspinules various in specimens of different species; maxillary palpus as in Figure 22. Adoral surface of labium (hypopharynx) with numerous, very fine, inwardly and anteriorly directed hairlike processes on each side of midline. Labium as in Figure 19; ligula short, very slightly protruded, less than 0.5 times length of labial palpus, very broad, truncate, moderately deeply emarginate medially into two short, broadly obtuse lateral lobes apically or emargination more shallowly incised, each lateral lobe finely and moderately densely pubescent in apicolateral half, each lobe with prominent to moderate sensilla within or lateral to emargination on each side of midline; labial palpus 2 articled, article 1 about 0.6 times length of 2, apical spine of article 2 markedly developed; seta near insertion of labial palpus moderately developed.

Thorax—Pronotum (fig. 24) transverse, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 moderately to well developed; Dc2 about 1.2–1.5 times length of Da2, lateral setae L2 and L3 present; ecdysial suture moderately well developed. Mesonotum (fig. 25) similar to pronotum except anterior setae reduced to microtrichous pores in slightly sclerotized anterior portion of tergum; discal setae Da2 and Dc2 present, Dc2 about 1.5–1.7 times length of Da2, Dd2 absent; lateral setae L2 and L3 absent, L5 present. Metanotum similar to mesonotum. Legs as in Figure 27; relatively long and slender, femur length to width ratio 3.1–3.3.

Abdomen—Abdominal terga I–VII (fig. 26) very markedly transverse, anterior margin slightly sclerotized, discal setae Da2, Db3, and Dc2 present, Da2 slightly developed, in posterior row between P1 and C6, Db3 moderately developed, in posterior row between P3 and P4, Dc2 slightly developed, discal; lateral seta L1 present. Abdominal tergum VIII (fig. 29) markedly produced posteromedially as broad lobe in association with well-developed tergal gland; chaetotaxy as in Figure 29, Da2 and Dc2 present as very small microtrichous pores; posterior seta P1 flattened, slightly brushlike, apex finely serrate, serrations incised less than 0.05 times length of seta (fig. 30). Tergal gland reservoir distinct, well developed, 0.7–0.9 times length of tergum; gland ducts with single loop irregularly developed or with partial second loop. Abdominal tergum IX–X as in Figure 28; urogomphus single articled, relatively long, 0.6–0.7 times length of tergum IX. Pseudopodium without hooks.

MATERIAL EXAMINED—*Agaricomorpha apacheana* (Seevers); 12, all instars, assoc.; New Mexico, 2.3 mi NE Cloudcroft, July 12, 1976, J. S. Ashe, ex *Fomitopsis pinicola*: *Agaricomorpha apacheana* (Seev.); 17, all instars; New Mexico,



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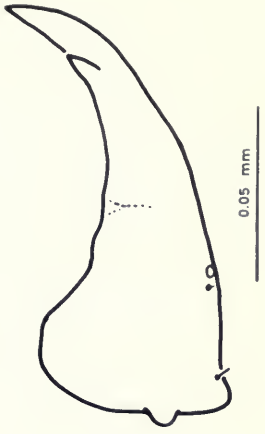

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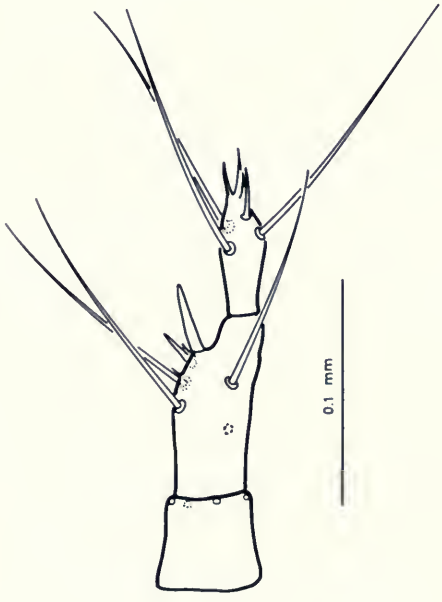

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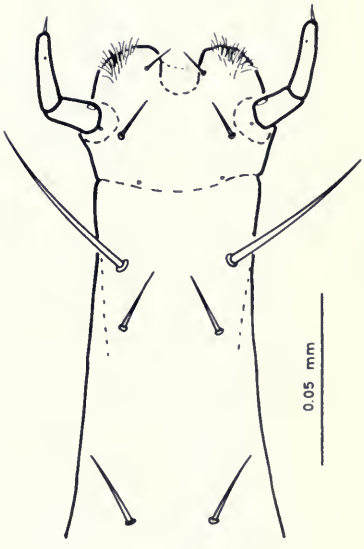

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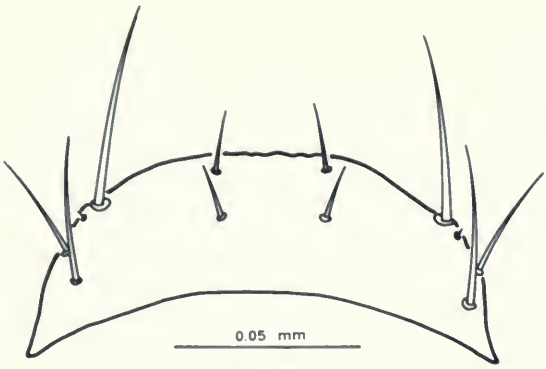
FIGS. 16–19. *Agaricomorpha apacheana* (Seevers), larval instar III. **16,** Head, dorsal aspect; **17,** mandible, ventral aspect; **18,** antenna, dorsal aspect; **19,** labium, ventral aspect.



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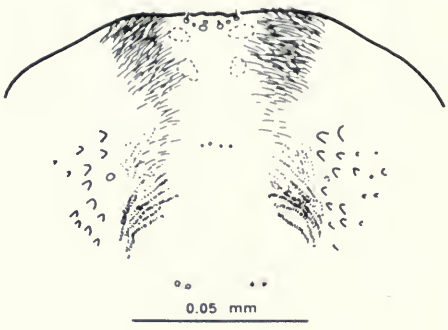

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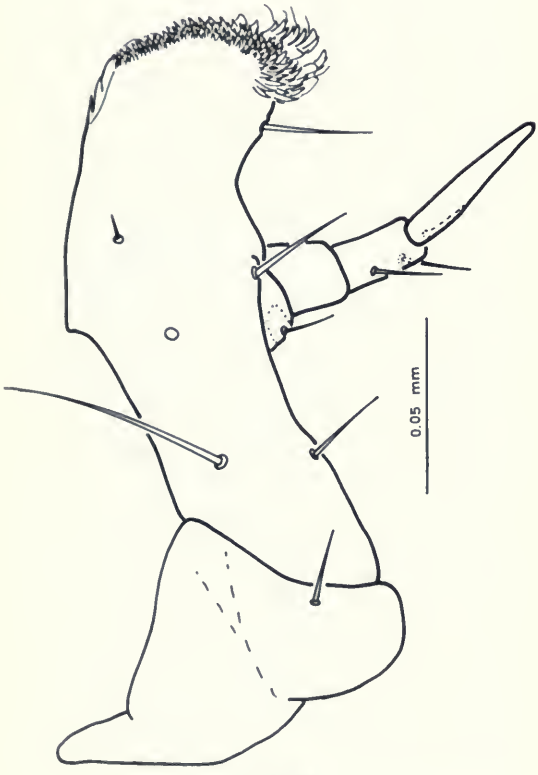

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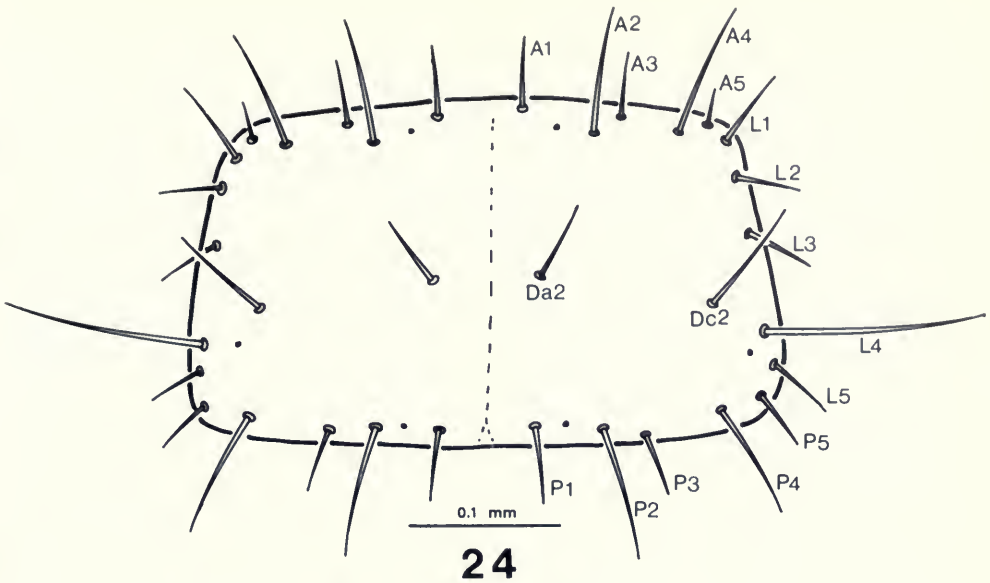
FIGS. 20–23. *Agaricomorpha apacheana* (Seevers), larval instar III. **20,** Labrum, dorsal aspect; **21,** labrum, adoral aspect (epipharynx); **22,** maxilla, ventral aspect; **23,** detail of mala of maxilla, dorsal aspect.



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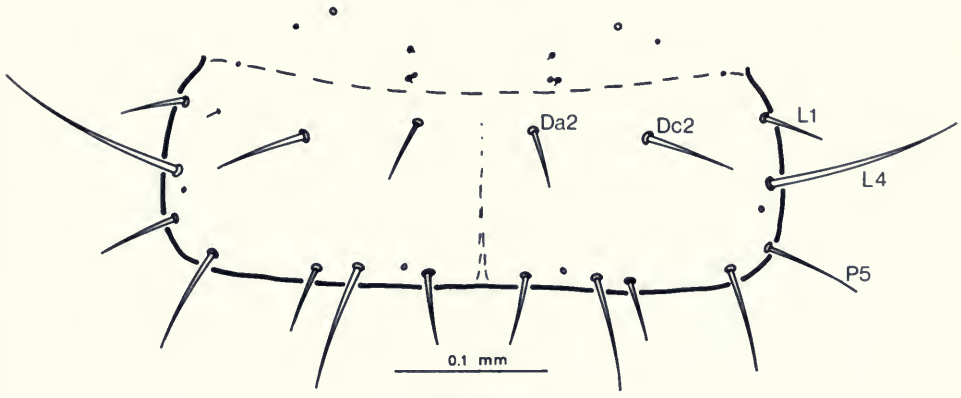

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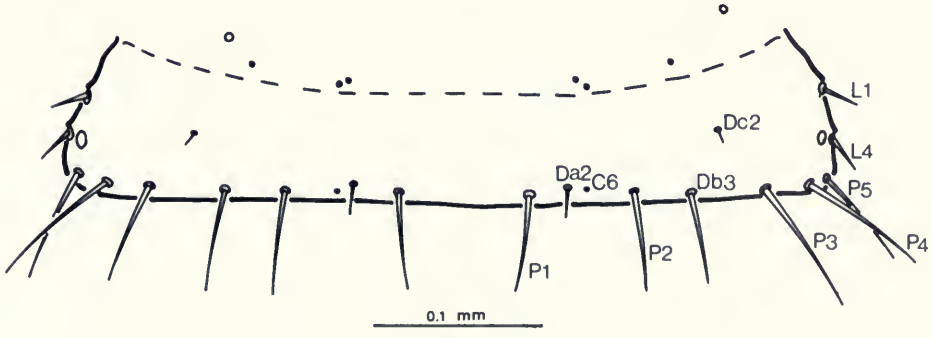

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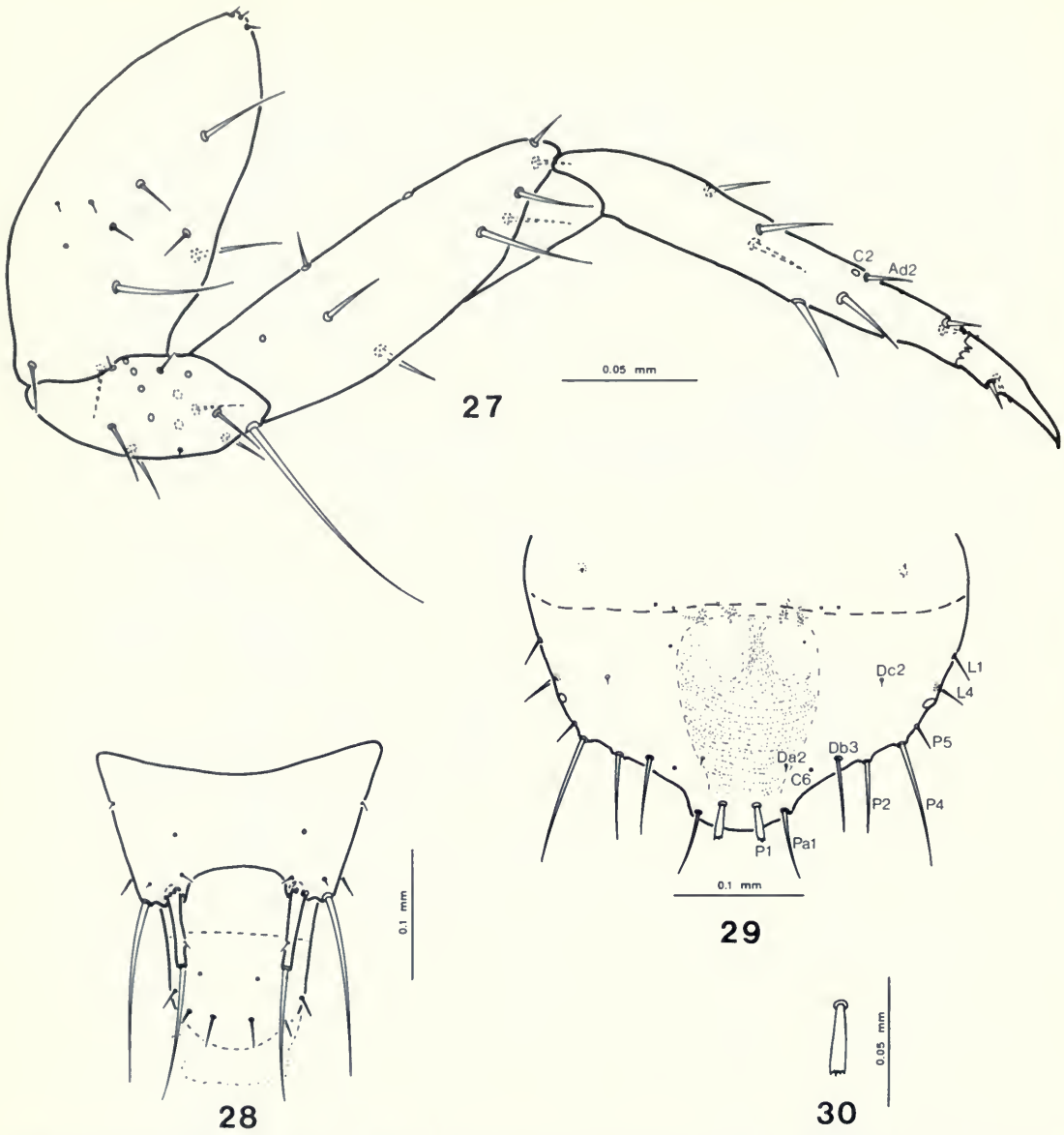
FIGS. 24–26. *Agaricomorpha apacheana* (Seevers), larval instar III. **24,** Pronotum; **25,** mesonotum; **26,** abdominal tergum I.



FIGS. 27–30. *Agaricomorpha apacheana* (Seevers), larval instar III. **27,** Proleg, anterior aspect; **28,** abdominal terga IX–X; **29,** abdominal tergum VIII; **30,** brushlike seta, P1 of abdominal tergum VIII, detail.

0.7 mi E Cloudcroft, September 28, 1975, J. S. Ashe, ex polypore on conifer log: *Agaricomorpha* undes. sp. 1 (very near *A. apacheana*); 23, all instars, assoc.; New Mexico, Bernadillo Co., Cibola Natl. For., Sandia Mtns., 14.6 mi N Cedar Crest, rd. 536, August 4, 1983, J. S. Ashe, ex *Fomes fomentarius*: *Agaricomorpha* undes. sp. 1; 17, all instars, assoc.; Arizona, Coconino Natl. For., San Francisco Peaks, 11 mi NW Flagstaff, Snowbowl rd., July 19, 1983, J. S. Ashe, ex *Fomes fomentarius*: *Agaricomorpha* undes. sp. 2; 8, instar III, assoc.; Mexico, Chiapas, 13.6 km SE Tolimán, 1600 m elev., July 11, 1979, J. S. Ashe, ex polypore on log: *Agaricomorpha* undes. sp. 3; 23, all instars, assoc.; Mexico, Jalisco, E slope Nevado de Colima, 9300′ elev., IX-21-1973, ex *Ganoderma*(?) on dead *Abies*, A. Newton (MCZ): *Agaricomorpha* undes. sp. 4; 36, all instars, assoc.; Arizona, Pima Co., Bogs Springs, August 11, 1978, M. A. Ivie, coll., ex *Polyporus* sp. (prob. *P. arcularius*).

DISCUSSION—Among gyrophaenine larvae, those

of *Agaricomorpha* can be distinguished from those of *Brachychara,* which they resemble in mouthpart structure and chaetotaxic features, by the characters in the key. Particularly distinctive among these is the more flattened body, presence of Da2 of abdominal terga I–VII in posterior row between P1 and C6, spatulate rather than brushlike posterior seta P1 of abdominal tergum VIII, and much longer urogomphi.

Apotypic features of larvae of *Agaricomorpha* provide strong evidence that this genus is the sister group to *Brachychara.* This conclusion is primarily a result of similarities of the mala of the maxilla, position of Da2 of abdominal terga I–VII in posterior row, and prominent setose sensillae on the ligula of larvae of both genera. This sister group relationship based on larval characteristics parallels that hypothesized by Ashe (1984) based on adult features. Apomorphic features shared by these two genera in combination with the paucity of apotypic features uniquely shared between larvae of *Agaricomorpha* and *Agaricochara* strongly support Ashe's (1984) decision to separate the known New World taxa then placed in *Agaricochara* into a new genus, *Agaricomorpha.*

Larvae of *Agaricomorpha* have been collected in association with adults from fruiting bodies of *Fomitopsis pinicola, Fomes fomentarius, Ganoderma*(?) sp. and *Polyporus* sp. (prob. *P. arcularius*), and other woody polypores on logs. Members of the genus appear to be limited to these woody or leathery polypore mushrooms on logs (see also Ashe, 1984). North American species are particularly common on various woody conk-forming mushrooms such as species of *Ganoderma, Fomitopsis,* and *Fomes.*

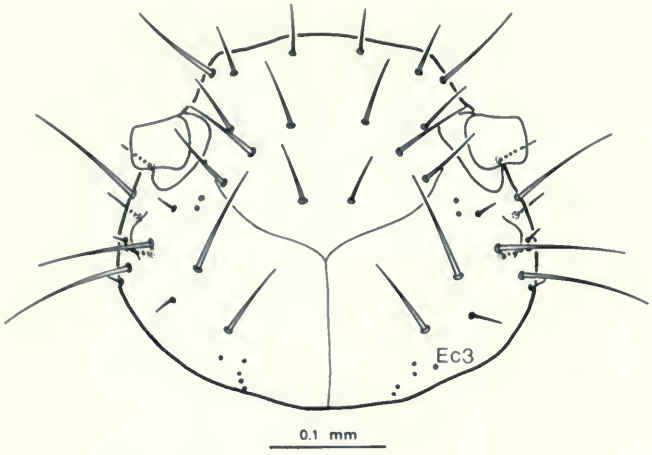
Larvae of *Agaricomorpha* have not been previously described.

Late Instar Larvae of *Brachychara* Sharp (Figures 31-45, 97-98)

DESCRIPTION—**General**—Length of mature larva 2.0–2.4 mm. General body form elongate, more or less parallel sided, robust, broadly oval in cross section. Color of mature larvae of available species whitish with terga light brown, abdominal tergum I lighter, whitish, sclerites of abdominal terga VII–X darker brown. Microsculpture absent except for very faint micropoints in distinct very short rows on sclerites of abdominal segments VII–X. Vestiture of long simple setae.

Head (Figure 31)—Length to width ratio of specimens of available species 0.8. Ocellus single on each side, small, inconspicuous. Ecdysial sutures well developed, distinct, lateral arms attaining antennal fossae. Chaetotaxy characteristic of subtribe, campaniform sensilla Ec3 present. Antenna as in Figure 33, 3 articled, relative lengths of articles of specimens of species available, article 1 about as long as wide, article 2 2.6 times as long as 1, article 3 0.5 times as long as 2; sensory appendage of antennomere 2 elongate, spinelike, about 1.6 times length of constricted portion of article 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 present, minute, and spinose, IIS1 moderately spinose, apex more or less acute, prominent, about 0.7 times length of sensory appendage, IIS2 spinose, present as very small spinule, about 0.1–0.2 times length of IIS2; solenidea of article 3 spinose, of similar size, not inflated or enlarged. Labrum as in Figure 36; chaetotaxy with Ld1 and Ld2 well developed, of similar size, setose. Epipharynx as in Figure 35. Mandibles (fig. 32) with subapical tooth moderately developed; lobe in molar area very slightly developed or absent; more distal seta of lateral half present as microtrichous pore, more proximal seta moderately developed. Maxilla (fig. 37) typical of subtribe; mala obliquely truncate with 8–10 rows of very small teeth in proximomedial 0.8 and a distinct raised area of small teeth in distal 0.2, more distal teeth not markedly larger than proximal teeth (fig. 37); apex of mala with single deeply emarginate foliose scale apically; lateral and apical surface of mala with several scalelike and more or less foliose lobes, teeth, or spatulate structures (fig. 38); base of adoral surface of mala with a few scattered microspicules near base of palpus and near mediolateral margin; maxillary palpus as in Figure 37. Adoral surface of labium (hypopharynx) with numerous, very fine, inwardly directly hairlike processes on each side of midline. Labium as in Figure 34; ligula short, very slightly protruded, less than 0.5 times length of labial palpus, very broad, truncate and broadly emarginate medially into two short lateral lobes apically, each lobe with prominent setose sensilla apicomedially and very small microspinose sensilla in emargination on each side of midline; labial palpus 2 articled, article 1 about 0.6 times length of article 2, apical spine markedly developed; seta near insertion of labial palpus large, prominent.

Thorax—Pronotum (fig. 39) transverse, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 moderately to well developed, Dc2 about 2.0 times



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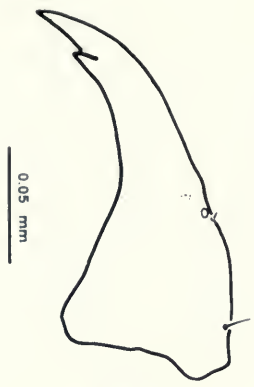

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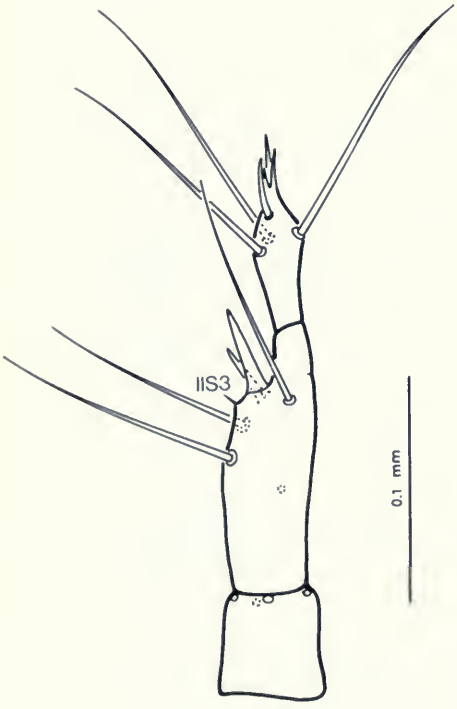

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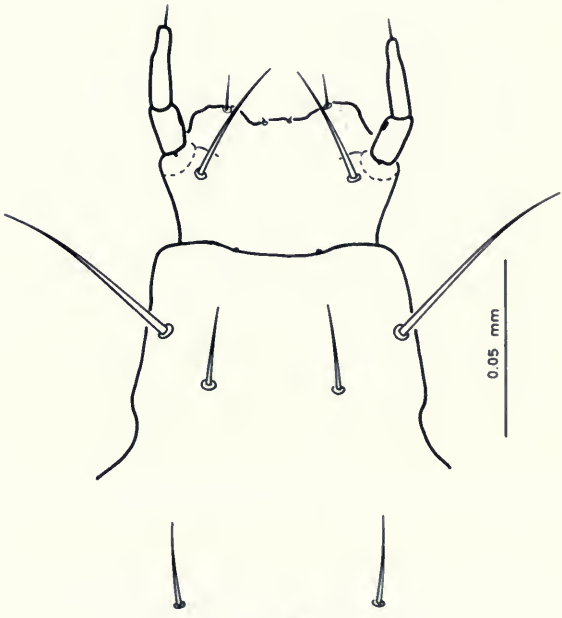

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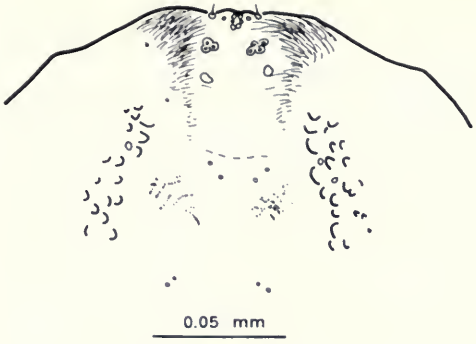
FIGS. 31–34. *Brachychara* species 1, larval instar III. **31,** Head, dorsal aspect; **32,** mandible, ventral aspect; **33,** antenna, dorsal aspect; **34,** labium, ventral aspect.



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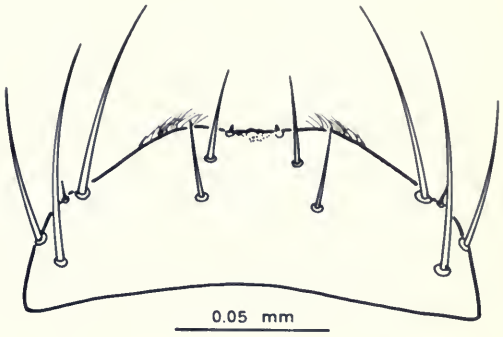

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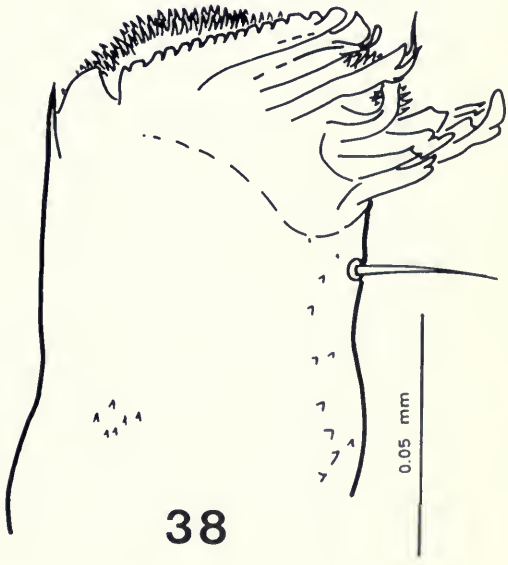

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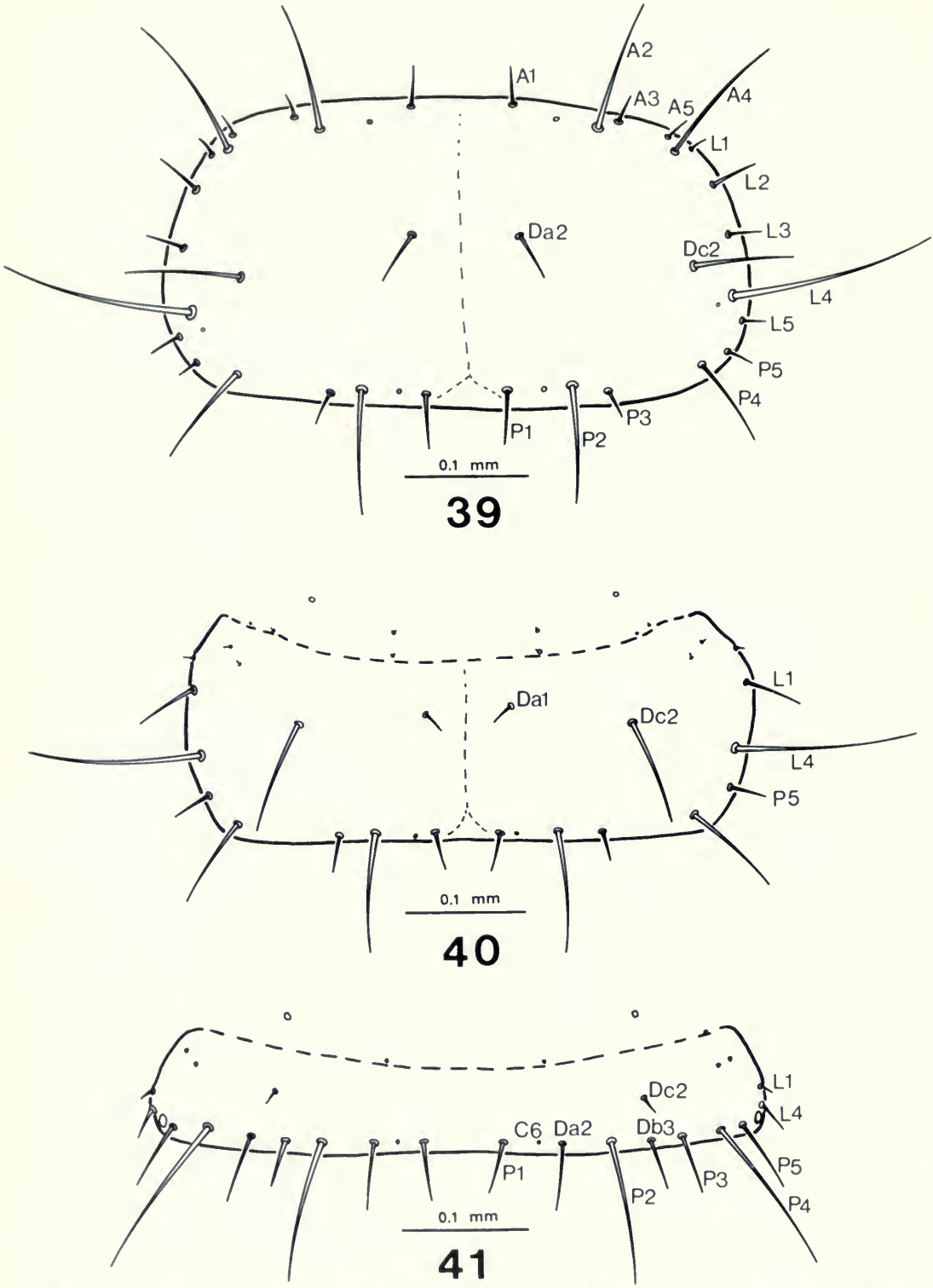
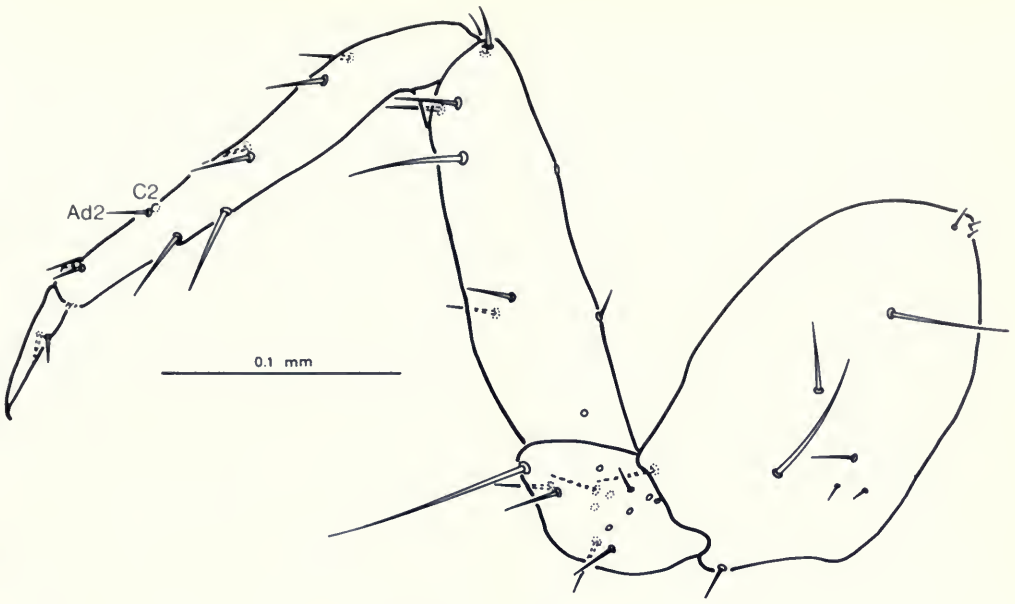
FIGS. 35–38. *Brachychara* species 1, larval instar III. **35,** Labrum, adoral aspect (epipharynx); **36,** labrum, dorsal aspect; **37,** maxilla, ventral aspect; **38,** mala of maxilla, detail, dorsal aspect.



FIGS. 39–41. *Brachychara* species 1, larval instar III. **39,** Pronotum; **40,** mesonotum; **41,** abdominal tergum I.



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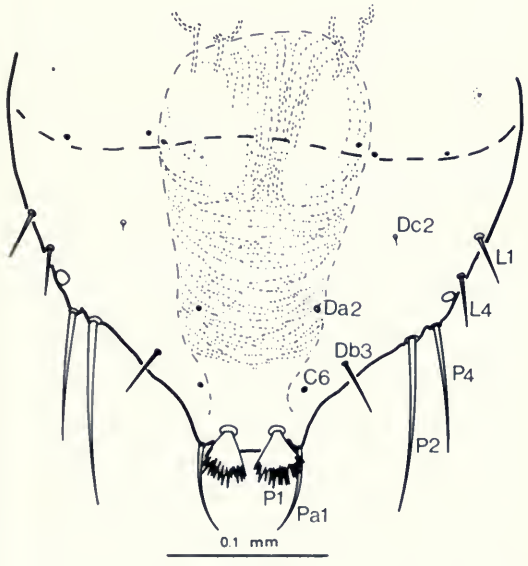

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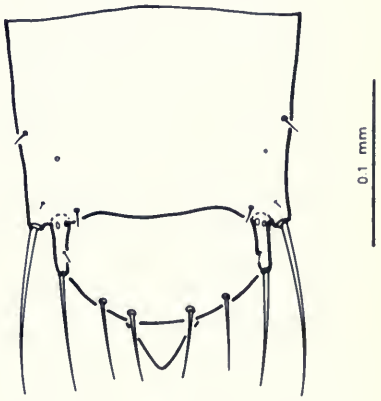

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FIGS. 42–45. *Brachychara* species 1, larval instar III. **42,** Proleg, anterior aspect; **43,** abdominal tergum VIII; **44,** brushlike seta, P1 of abdominal tergum VIII, detail; **45,** abdominal terga IX–X.

length of Da2, lateral setae L2 and L3 present; ecdysial suture well developed, prominent. Mesonotum (fig. 40) similar to pronotum except anterior setae reduced to microtrichous pores in slightly sclerotized anterior portion of tergum; discal setae Da2 and Dc2 present, Da2 slightly developed, Dc2 very large, 3.0–4.0 times length of Da2, Dd2 absent; lateral setae L2 and L3 absent, L5 absent. Metanotum similar to mesonotum. Legs as in Figure 42; relatively long and slender, femur length to width ratio 3.9–4.0.

Abdomen—Abdominal terga I–VII (fig. 41) very markedly transverse, anterior margin slightly sclerotized; discal setae Da2, Db3, and Dc2 present, Da2 moderately developed, in posterior row between C6 and P2, Db3 moderately developed, in posterior row between P3 and P4, Dc2 slightly developed, discal; lateral seta L1 present. Abdominal tergum VIII (fig. 43) markedly produced posteromedially as a broad lobe in association with well-developed tergal gland; chaetotaxy as in Figure 43, Da2 present as pore, Dc2 very small, present as microtrichous pore; posterior seta P1 brushlike, very broad with numerous serrations, serrations incised 0.3–0.5 times length of seta (fig. 44). Tergal gland reservoir distinct, well developed, about 1.0 times length of tergum VIII; gland ducts with single loop irregularly developed (fig. 43). Abdominal terga IX–X as in Figure 45; urogomphi single articled, short, about 0.3 times length of tergum IX. Pseudopodium without hooks.

MATERIAL EXAMINED—*Brachychara* sp. 1; 47, all instars, assoc.; Panama, Canal Zone, Cerro Galera, 1000′ elev., VI-23-1976, A. Newton, on surface white polypore tree fungus (MCZ): *Brachychara* sp. 2; 3, instar III, assoc.; Mexico, Veracruz, 3.1 mi W Sontecomapan, May 7, 1977, tropical deciduous association, 200 m elev., J. S. Ashe, ex leathery, shelving polypore on log.

DISCUSSION—Larvae of *Brachychara* can be distinguished from those of *Agaricomorpha,* which they resemble, and from those of all other gyrophaenines by characters in the key. Particularly distinctive among *Brachychara* larvae are the robust body form, the distinctive raised area of small teeth in distal 0.2 of the mala, presence of discal seta Da2 of abdominal terga I–VII in posterior row between C6 and P2, posterior seta P1 of abdominal tergum VIII very broad and brushlike, and the very short urogomphi. In addition to these features, abdominal tergum I of all late instar larvae of *Brachychara* examined were distinctly paler than other terga. This gives the impression that these larvae are transversely crossed by a light band behind the thorax. No other gyrophaenine larvae examined had this feature.

Larvae of *Brachychara,* and to a lesser extent those of *Agaricomorpha* and *Agaricochara,* are unusual in that though they exhibit a diversity of plesiotypic characteristics, particularly in chaetotaxic features, in comparison with *Gyrophaena* and related genera, they have the most complex and presumably highly derived mouthparts among known gyrophaenine larvae. They are considerably more complex than those of *Gyrophaena* and related genera both in number and density of spines on the mala as well as in elaboration of spinelike and spatulate scales associated with the distolateral surface of the mala (see Structural Features). Such highly derived features may be associated with requirements of the host substrate.

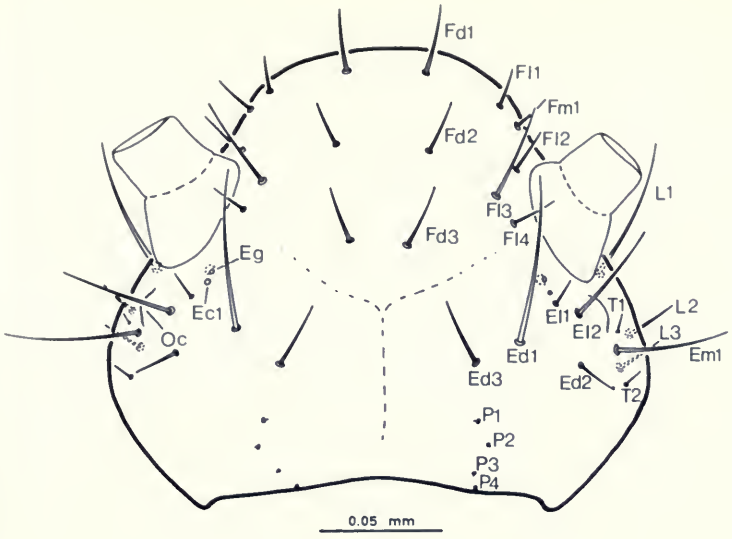
Both larvae and adults of *Brachychara* have been collected in association with leathery and woody polypore mushrooms on logs. Other data (Ashe, 1984, unpubl. data) indicate that members of *Brachychara* are characteristic inhabitants of such fungi.

Immatures of *Brachychara* have not been previously described.

Late Instar Larvae of *Eumicrota* Casey (Figures 46–65, 102)

DESCRIPTION—**General**—Length of mature larva 1.1–1.7 mm. General body form elongate, slightly flattened, broadest at intermediate abdominal segments. Color of mature larva whitish with sclerites of abdominal segments VII–X dark brown in specimens of species examined. Microsculpture absent except for micropoints on terga and sterna of abdominal segments IX–X, micropoints in distinct but very short straight to semilunulate rows or scattered. Vestiture of long simple setae.

Head (Figure 46)—Length to width ratio among specimens of available species 0.7–0.8. Ocellus single on each side, small to very small, inconspicuous. Ecdysial sutures slightly developed, lateral arms attaining antennal fossae. Chaetotaxy characteristic of subtribe, campaniform sensilla Ec3 absent. Antenna as in Figure 48, 3 articled, relative lengths of articles various in specimens of different species; sensory appendage on antennomere 2 elongate, very slender, spinelike, about 2.1–2.3 times as long as constricted portion of article 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 present, very minute and spinose, IIS1 digitiform and slightly rounded at apex, 0.30–0.45



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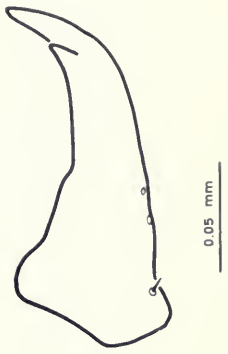

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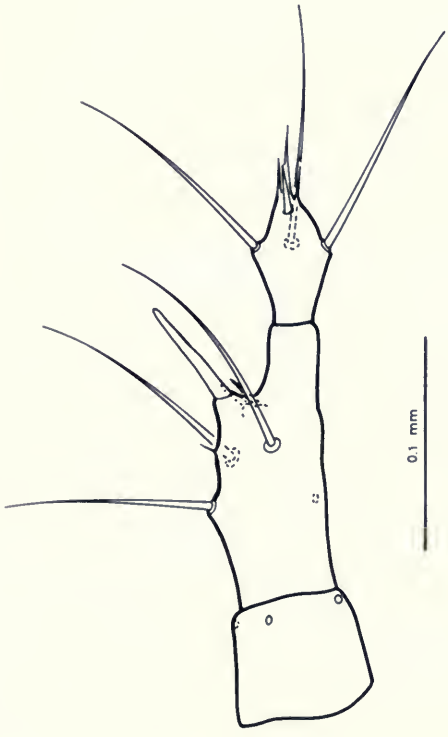

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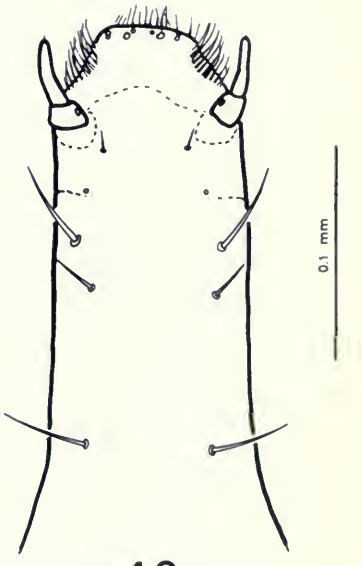

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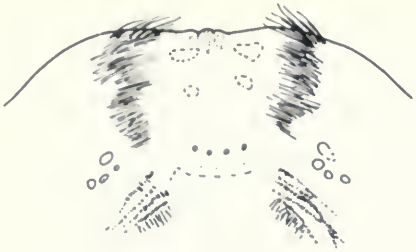
FIGS. 46–49. *Eumicrota corruscula* (Erichson), larval instar III. **46,** Head, dorsal aspect; **47,** mandible, ventral aspect; **48,** antenna, dorsal aspect; **49,** labium, ventral aspect.



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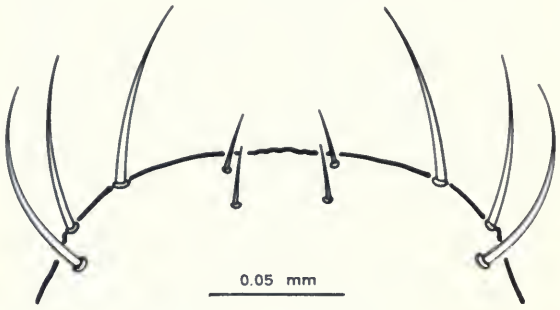

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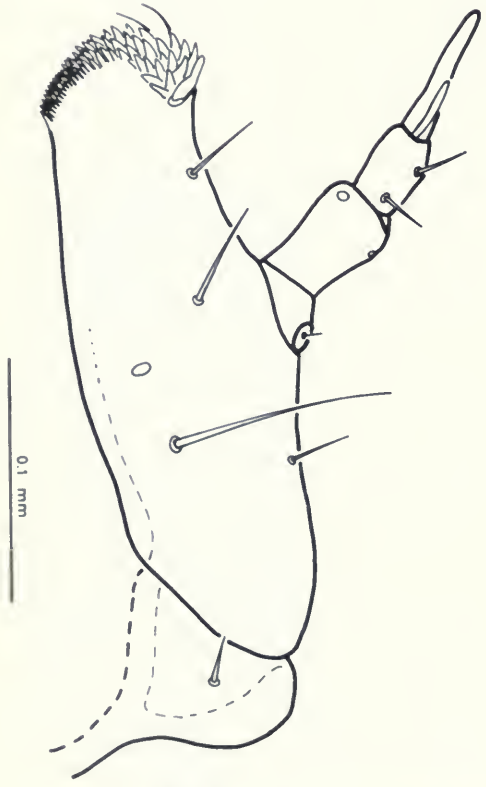

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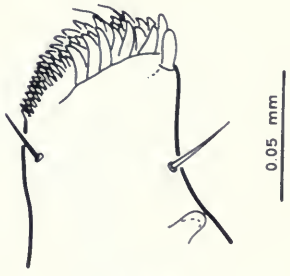

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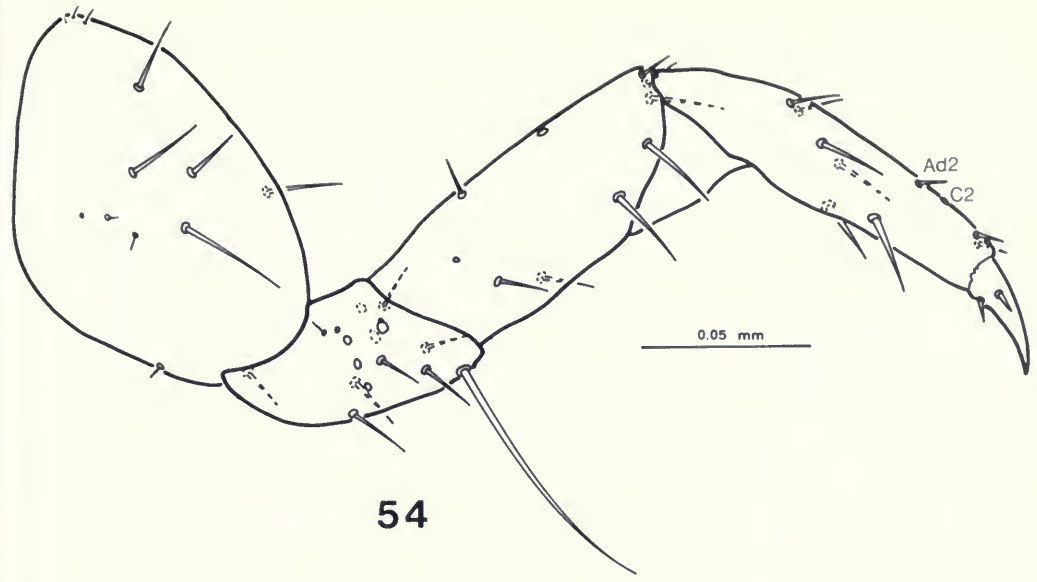
FIGS. 50–53. *Eumicrota corruscula* (Erichson), larval instar III. **50,** Labrum, adoral aspect (epipharynx); **51,** labrum, dorsal aspect; **52,** maxilla, ventral aspect; **53,** mala of maxilla, detail, dorsal aspect.



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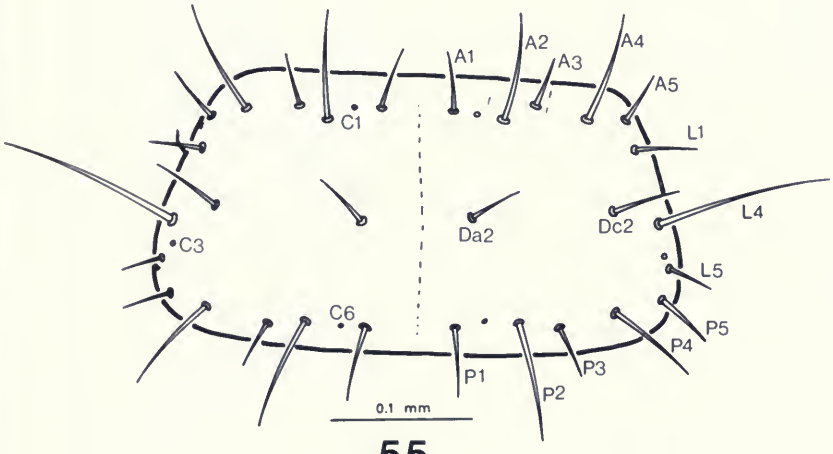

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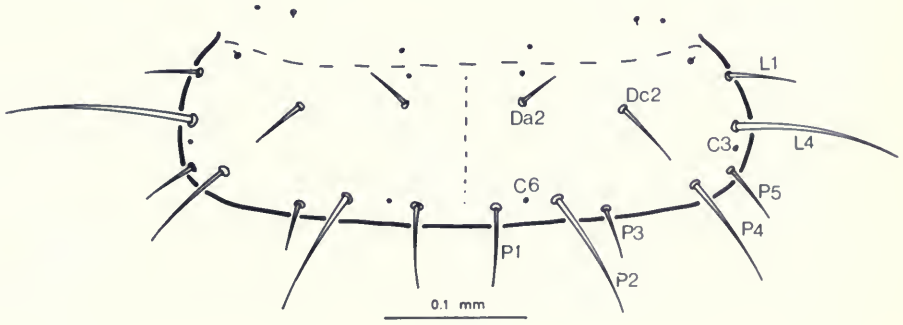

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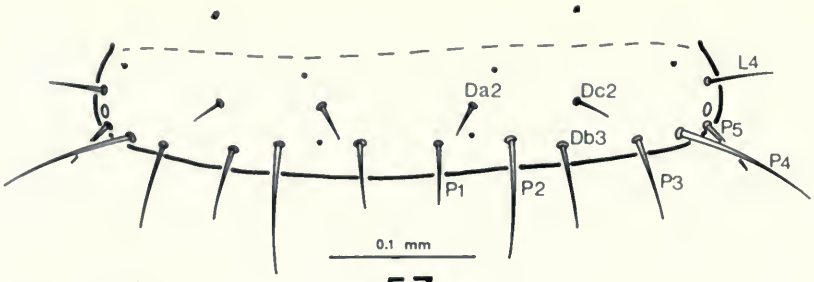
FIGS. 54–56. *Eumicrota corruscula* (Erichson), larval instar III. **54,** Proleg, anterior aspect; **55,** pronotum; **56,** mesonotum.



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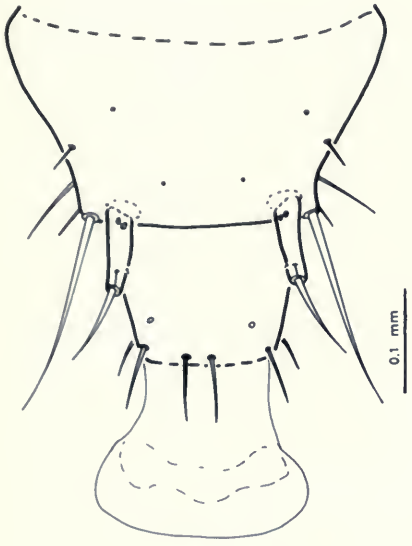

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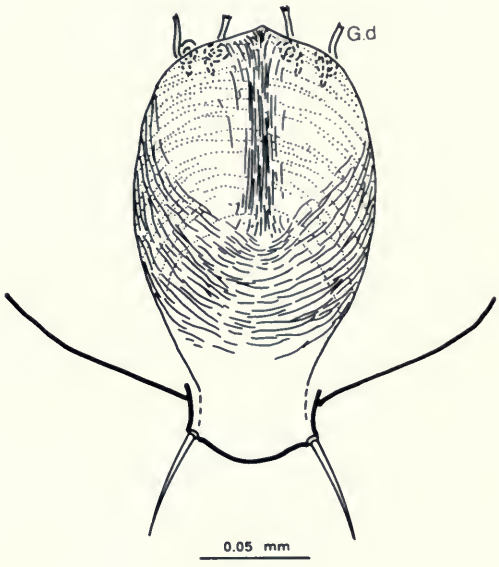

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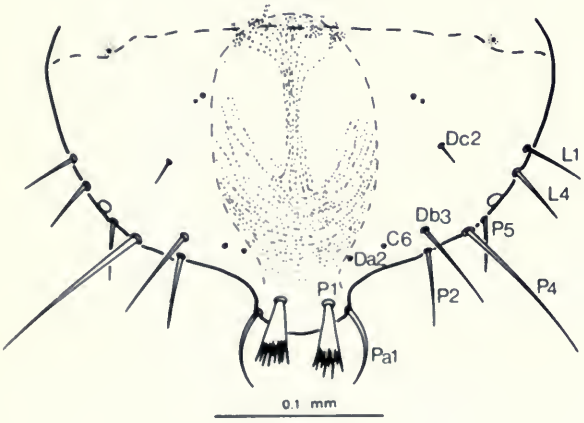

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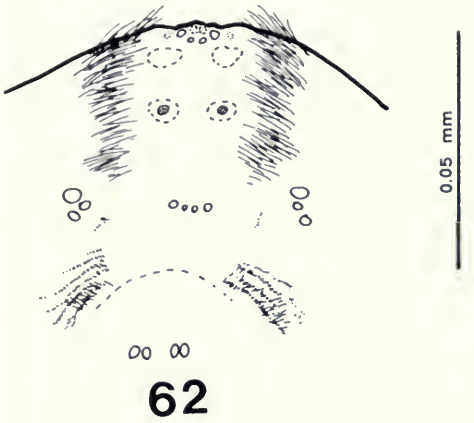
FIGS. 57–61. *Eumicrota corruscula* (Erichson), larval instar III. **57,** Abdominal tergum I; **58,** abdominal terga IX–X; **59,** tergal gland reservoir of abdominal segment VIII, detail; **60,** abdominal tergum VIII; **61,** brushlike seta, P1 of abdominal tergum VIII, detail.



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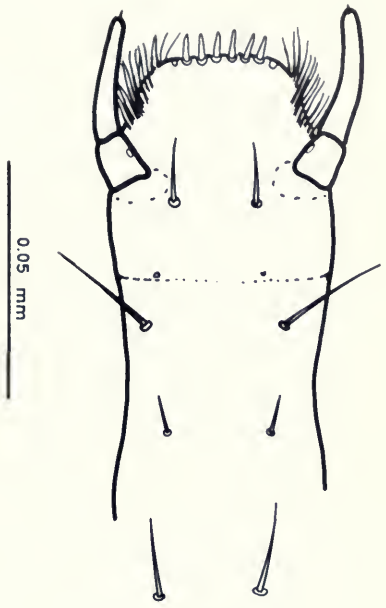

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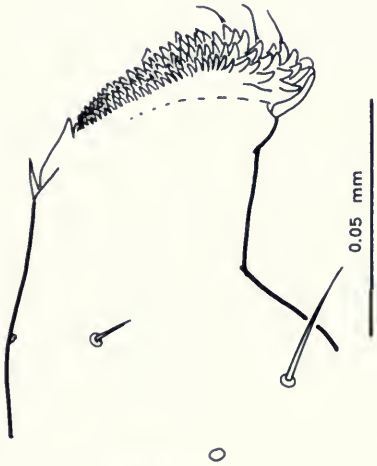

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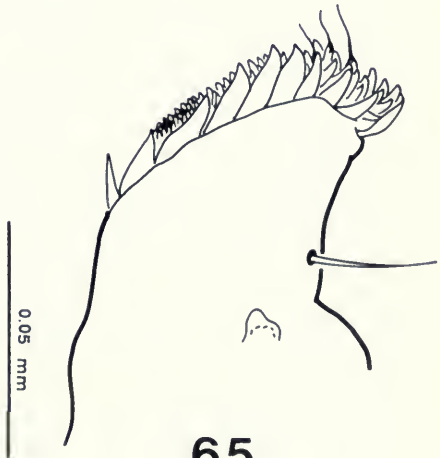

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FIGS. 62–65. *Eumicrota cornuta* Casey, larval instar III. **62,** Labrum, adoral aspect (epipharynx); **63,** labium, ventral aspect; **64,** mala of maxilla, ventral aspect; **65,** mala of maxilla, dorsal aspect.

times length of sensory appendage, IIS2 spinose, 0.9–1.0 times length of IIS1; solenidea of antennomere 3 spinose, pointed apically, not enlarged or inflated. Labrum as in Figure 51; setation with Ld1 and Ld2 of similar size, moderately developed, setose. Epipharynx as in Figures 50 and 62. Mandibles (fig. 47) with subapical tooth moderately developed; lobe in molar area slightly developed; more distal seta in lateral basal half reduced to pore, more proximal seta small. Maxilla (fig. 52) typical of subtribe; mala (figs. 52, 64) obliquely truncate with 4–5 rows of moderate to small teeth, teeth largest distally and smaller more proximally; apex of mala with deeply emarginate foliose scale distally; lateral surface of mala with 4–5 moderate scalelike teeth or lobes externally (figs. 53, 65); base of adoral surface of mala with small to large papillate lobe laterally near palpus insertion and without microspinules near medial border (figs. 53, 65); maxillary palpus as in Figure 52, relative lengths of articles various among specimens of different species. Adoral surface of labium (hypopharynx) with numerous inwardly directed hairlike processes on each side of midline. Labium as in Figures 49 and 63; ligula short, slightly protruded, length equal to or less than length of labial palpus, truncate and slightly rounded apically, not or only very slightly emarginate apically, without prominent spinose or setose sensilla on each side of midline, with (fig. 63) or without (fig. 49) apical peglike sensory elements; lateral surface of ligula with numerous fine hairs; labial palpus 2 articled, article 1 less than 0.5 times length of 2, apical spine slightly developed; seta near insertion of labial palpus small to moderate in size.

Thorax—Pronotum (fig. 55) transverse, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 moderately to well developed, of similar size, lateral setae L2 and L3 absent; ecdysial suture faint to moderately developed. Mesonotum (fig. 56) similar to pronotum except anterior setae reduced to microtrichous pores in slightly sclerotized anterior portion of tergum; discal setae Da2 and Dc2 present, well developed, of similar size, Dd2 absent; lateral setae L2, L3, and L5 absent. Metanotum similar to mesonotum. Legs as in Figure 54; relatively short and stocky, femur length to width ratio 2.0–2.4.

Abdomen—Abdominal terga I–VII (fig. 57) markedly transverse, anterior margin slightly sclerotized; discal setae Da2, Db3, and Dc2 present, well developed, of similar size, Da2 not in posterior row, Db3 in posterior row between P3 and P4; lateral seta L1 absent. Abdominal tergum VIII (fig. 60) markedly produced posteromedially as broad lobe in association with well-developed tergal gland; chaetotaxy as in Figure 60, discal seta Da2 reduced to pore, Dc2 present, slightly developed; posterior seta P1 brushlike, serrations incised 0.35–0.45 times length of seta (fig. 61). Tergal gland reservoir distinct, well developed, about as long as length of tergum VIII; gland ducts with markedly developed loop (fig. 59). Abdominal terga IX–X as in Figure 58; urogomphi single articled, about 0.5–0.6 times length of tergum IX. Pseudopodium without hooks.

MATERIAL EXAMINED—*Eumicrota cornuta* Casey; 10, instar III, assoc.; Dominican Republic, Barahona, 30-V-80, ex *Pleurotus calyx* (Speg.) Sing., 4200′ elev., coll. G. Mazurek: *Eumicrota corruscula* (Erichson); > 500, all instars, assoc.; Illinois, Cook Co., Palos Hills, 26-VI-82, L. E. Watrous, ex *Polyporus* sp. (near *P. alveolaris*): *Eumicrota spinosa* (Seevers); > 400, all instars, assoc.; New Mexico, Santa Fe Co., Sangre de Cristo Range, 6.5 mi NE Santa Fe, hwy 475, July 28, 1984, J. S. Ashe, ex brown, fan-like polypore on ground under conifers.

DISCUSSION—Larvae of *Eumicrota* can be distinguished from those of all other gyrophaenines by characters in the key. Among members of the "Gyrophaena" lineage, larvae of which are very similar, known larvae of *Eumicrota* may be distinguished from those of *Phanerota,* which they most closely resemble, by their smaller size, smaller ocellus, and proximolateral border of mala without microspinules. In addition, separation of known hosts of these two genera aids in identification of similar larvae. Larvae of *Phanerota* are known only from fleshy gilled mushrooms, whereas those of *Eumicrota* are known only from fleshy polypores or more persistent gilled mushrooms on logs. Although knowledge of host ranges of members of these two genera is admittedly very incomplete, all available evidence from both larval and adult collection records suggests that the range of preferred hosts of members of these two genera is within different host types (see Ashe, 1984). A further distinctive characteristic of late instar larvae of *E. corruscula* (Erichson) and *E. cornuta* Casey is the conspicuously dark brown color of abdominal segments VIII–IX, a feature not found among other known gyrophaenine larvae.

Based on larval characteristics, *Eumicrota* is hypothesized to be the sister group of *Phanerota*;

however, adult features do not support this supposition (see discussion under *Phanerota,* Phylogenetic Analysis).

Both adults and larvae of *Eumicrota* have been most commonly collected on fleshy to leathery polypores, though those of *E. cornuta* were found on a persistent gilled mushroom on a log.

Larvae of *Eumicrota* have not been previously described.

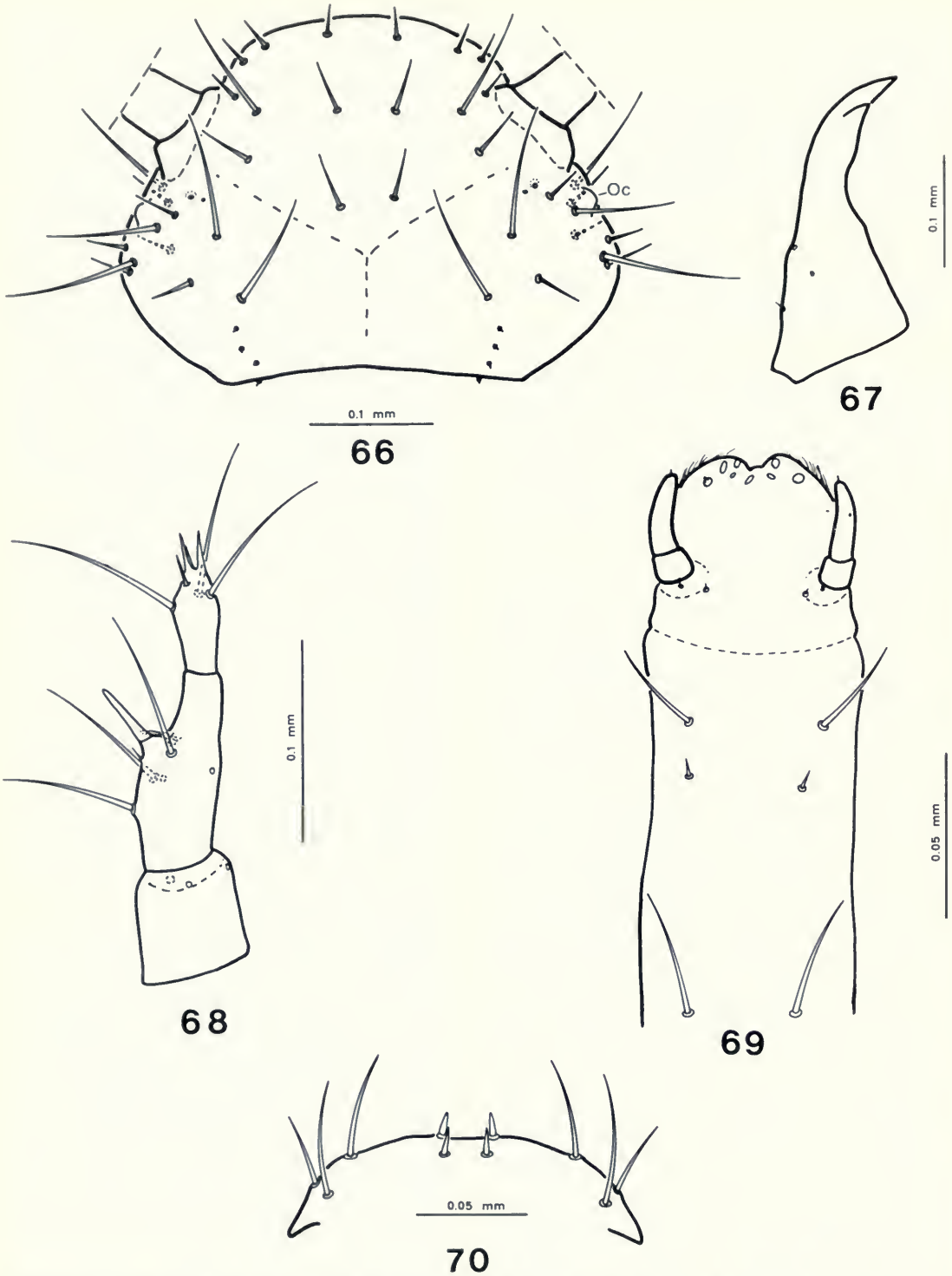
Late Instar Larvae of *Gyrophaena* Mannerheim (Figures 66-81, 100-101)

DESCRIPTION—**General**—Length of mature larva 2.3–4.2 mm. General body form elongate, slightly flattened, broadest at mesonotum and intermediate abdominal segments. Color of mature larva white to light gray-brown dorsally. Microsculpture absent or with scattered micropoints on various terga of abdominal segments III–X. Vestiture of long simple setae.

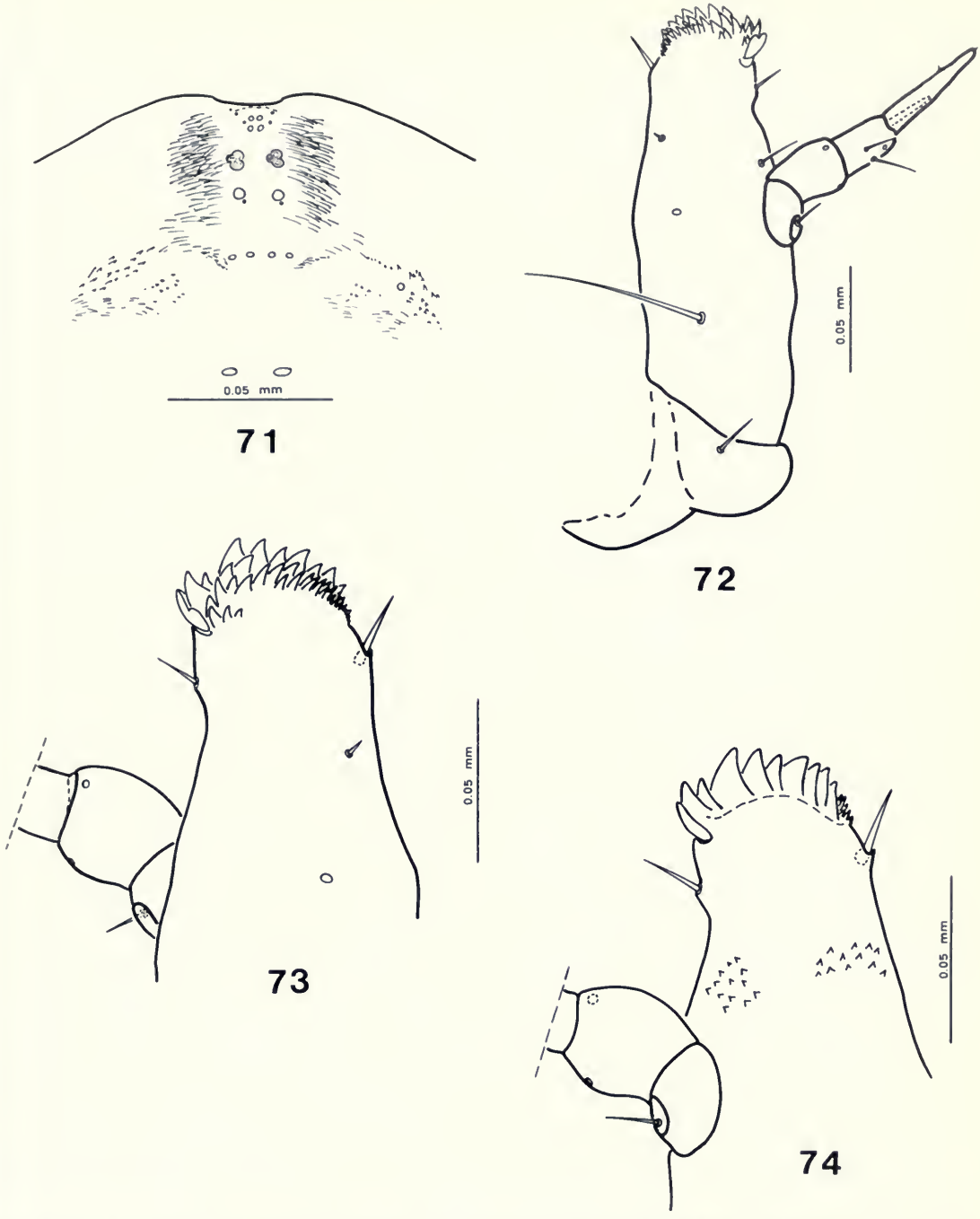
Head (Figure 66)—Length to width ratio various among specimens of available species, range 0.72–0.89. Ocellus single on each side, small to very small, inconspicuous. Ecdysial sutures slightly to well developed, lateral arms attaining antennal fossae. Chaetotaxy characteristic of subtribe; campaniform sensilla typical of subtribe, Ec3 absent. Antenna as in Figure 68, 3 articled; relative lengths of articles various in specimens of different species; sensory appendage on antennomere 2 elongate, spinelike, tapered uniformly from base to more or less acute apex, slightly curved in specimens of a few species, about 0.7–1.2 times length of constricted portion of antennomere 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 present, very small to minute and spinose, IIS1 digitiform and rounded at apex, 0.25–0.50 times length of sensory appendage, IIS2 spinose, 0.25–0.65 times length of IIS1; solenidea of antennomere 3 spinose, pointed apically, not enlarged or inflated. Labrum as in Figure 70; setation with Ld1 and Ld2 of similar size, relatively short and stubby, or more normal sized. Epipharynx as in Figure 71. Mandibles (fig. 67) with subapical tooth moderately developed, broad lobe in molar area slightly developed; more distal seta of lateral basal half reduced to pore, more proximal seta very small. Maxilla (fig. 72) typical of subtribe; mala (figs. 73–74) obliquely truncate with 3–4 rows of moderately large to small teeth, teeth markedly larger distally and smaller more proximally; apex of mala with single deeply emarginate foliose scale distally; lateral surface of mala without additional scalelike teeth, lobes, or spatulate structures; base of adoral surface of mala with small patch of microspinules on each side of midline (fig. 74), number of microspinules various in specimens of different species; maxillary palpus as in Figure 72, relative lengths of articles various in specimens of different species. Adoral surface of labium (hypopharynx) various, with few to many inwardly directed hairlike processes. Labium as in Figure 69; ligula short, slightly protruded, not as long or only slightly longer than labial palpus, broadly rounded, slightly to moderately emarginate apically, without prominent spinose or setose sensilla on each side of midline, without apical peglike sensilla, lateral surface without numerous fine hairs; labial palpus 2 articled, article 1 less than 0.5 times length of 2, apical spine slightly to moderately developed; seta near insertion of labial palpus very small to present as microtrichous pore.

Thorax—Pronotum (fig. 75) transverse, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 of similar size, lateral setae L2 and L3 absent; campaniform sensilla C1 present or absent; ecdysial suture faint or moderately developed. Mesonotum (fig. 76) similar to pronotum except anterior setae reduced to microtrichous pores in slightly sclerotized anterior portion of tergum; discal setae Da2 and Dc2 present, well developed, of similar size, Dd2 absent; lateral setae L2, L3, and L5 absent. Metanotum similar to mesonotum. Legs as in Figure 77; relatively short and stocky, femur length to width ratio 2.0–2.5, various among specimens of different species.

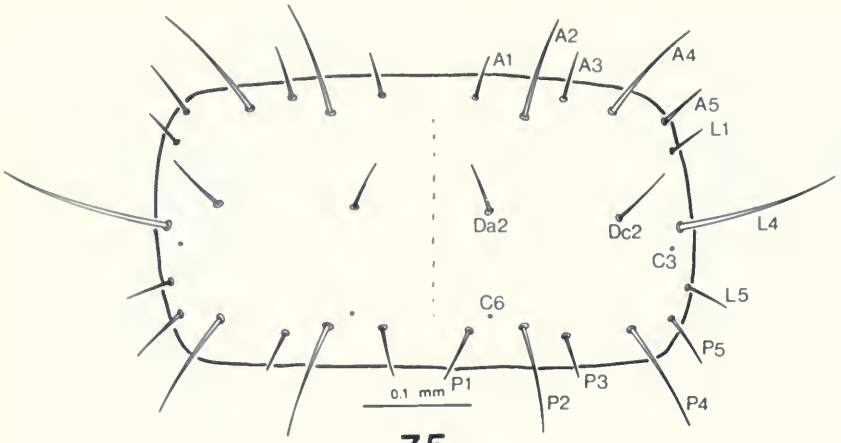
Abdomen—Abdominal terga I–VII (fig. 78) markedly transverse, anterior margin slightly sclerotized; discal setae Da2, Db3, and Dc2 present, well developed, of similar size, Da2 not in posterior row, Db3 in posterior row between P3 and P4. Abdominal tergum VIII (fig. 80) markedly produced posteromedially as broad lobe in association with well-developed tergal gland; chaetotaxy as in Figure 80, Da2 and Dc2 present, moderately developed; posterior seta P1 brushlike, deeply divided 0.7–0.9 distance to base into thin filamentus lobes (fig. 81) or serrations less deeply incised (0.5–0.7 distance to base). Tergal gland reservoir distinct, well developed, 0.35–1.1 times length of tergum VIII; gland ducts with single well-developed loop. Abdominal tergum IX–X as in Figure 79. Urogomphi single articled, about 0.5–



FIGS. 66–70. *Gyrophaena nana* Paykull, larval instar III. **66,** Head, dorsal aspect; **67,** mandible, ventral aspect; **68,** antenna, dorsal aspect; **69,** labium, ventral aspect; **70,** labrum, dorsal aspect.



FIGS. 71–74. *Gyrophaena nana* Paykull, larval instar III. **71,** Labrum, adoral aspect (epipharynx); **72,** maxilla, ventral aspect; **73,** mala of maxilla, ventral aspect; **74,** mala of maxilla, dorsal aspect.



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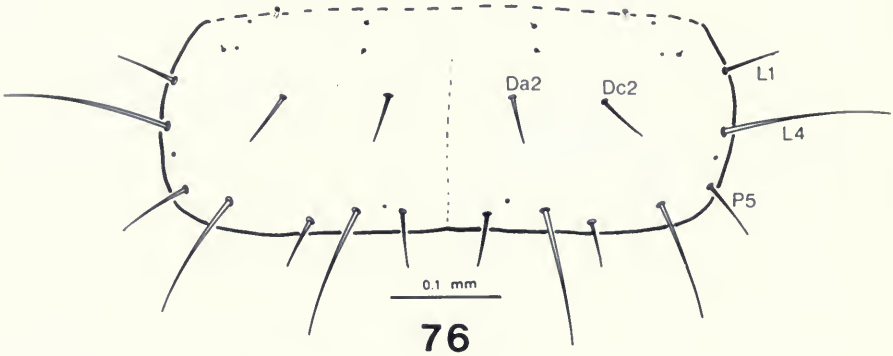

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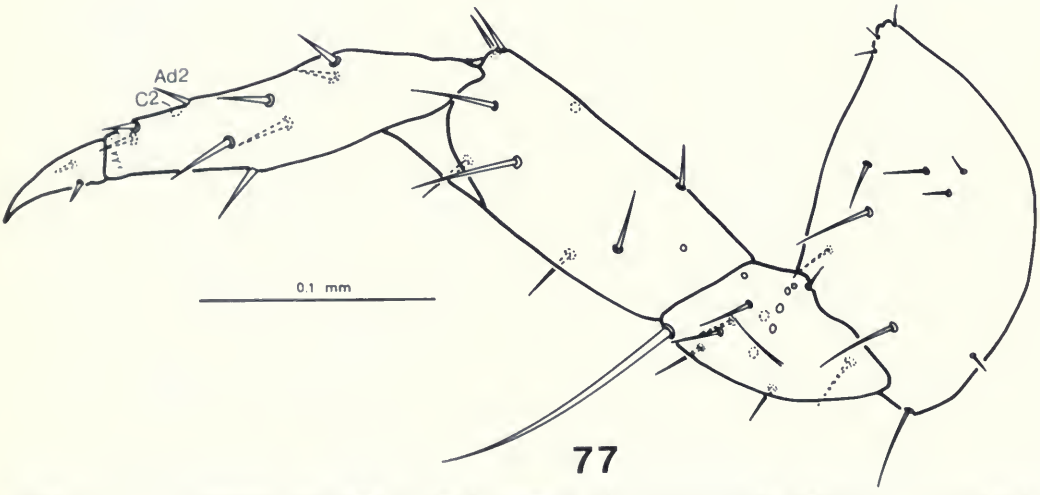

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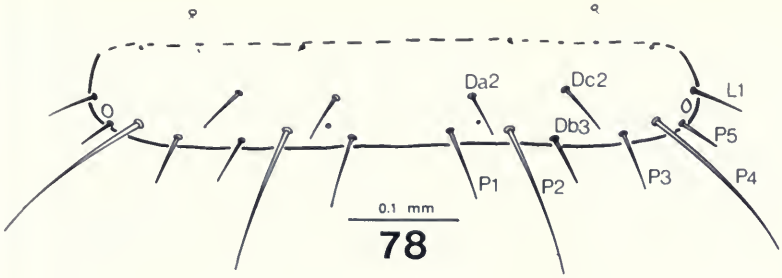
FIGS. 75–77. *Gyrophaena nana* Paykull, larval instar III. **75,** Pronotum; **76,** mesonotum; **77,** proleg, anterior aspect.



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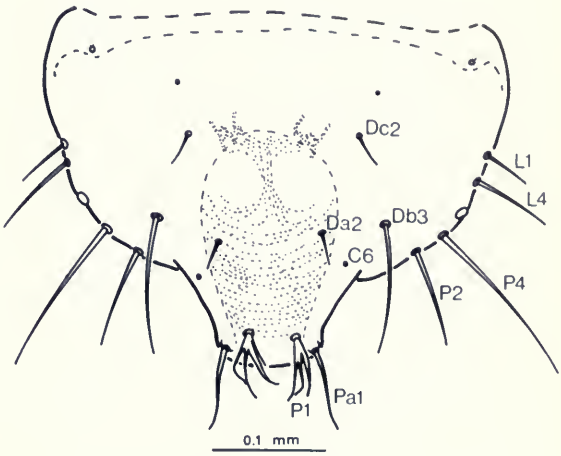

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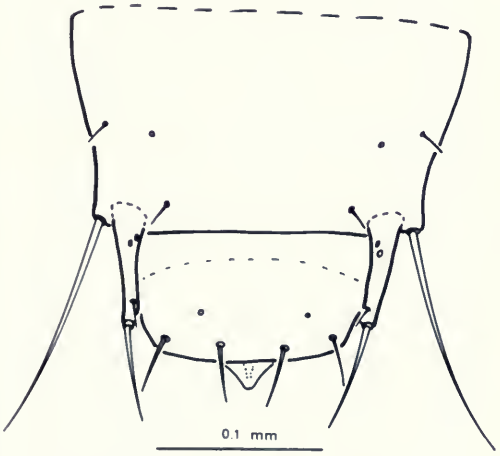

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FIGS. 78–81. *Gyrophaena nana* Paykull, larval instar III. **78,** Abdominal tergum I; **79,** abdominal terga IX–X; **80,** abdominal tergum VIII; **81,** brushlike seta, P1 of abdominal tergum VIII, detail.

0.7 times length of tergum IX, various in specimens of different species. Pseudopodium without hooks.

MATERIAL EXAMINED—*Gyrophaena affinis* Sahlberg; >100, all instars, assoc.; New Mexico, Santa Fe Co., Sangre de Cristo Range, 6.5 mi. NE Santa Fe, hwy 475, mixed conifer association, July 28, 1984, J. S. Ashe, ex *Collybia* sp.: *Gyrophaena affinis* Sahlb.; 6, instar III, ex ovo; Canada, Alberta, Edmonton, S bank North Sask. River, June 16, 1976, J. S. Ashe, ex *Collybia* sp.: *Gyrophaena affinis* Sahlb.; 17, all instars, assoc.; Canada, Al-

berta, Edmonton, S bank North Sask. River, June 26, 1976, J. S. Ashe, ex *Collybia cylindrospora*: *Gyrophaena arizonae* Seevers; 3, instar III, assoc.; Arizona, Coconino Co., Coconino Natl. For., Mogollon Mesa, 23.5 mi N Payson, hwy 87, August 7, 1983, J. S. Ashe, ex *Polyporus* sp.: *Gyrophaena barbari* Seevers; 4, instar III, assoc.; Arizona, Navajo Co., Sitgraves Natl. For., 47.8 mi E Payson, hwy 260, August 6, 1983, J. S. Ashe, ex Cortinariaceae: *Gyrophaena gentilis* Erichson; 37, all instars, assoc.; Kent, Lyminge Forest, ex *Tricholomopsis rutilans*, 21.IX.1974, I. M. White (BMNH): *Gyrophaena keeni* Casey; 44, instar III, reared; Canada, Alberta, Swan Hills, 54°42′N 115°49′W, 3750′ elev., August 10, 1977, J. S. Ashe, ex *Pholiota terrestris*: *Gyrophaena nana* Paykull; 23, instar III, reared; Canada, Alberta, George Lake, 53°57′N 114°06′W, July 24, 1979, J. S. Ashe, ex *Cortinarius* sp.: *Gyrophaena pulchella* Heer; 58, instar III, assoc.; Kinloch, Rhum, 26/8/81, fungus (BMNH): *Gyrophaena* sp. (prob. *G. modesta* Casey) (pulchella group); >100, all instars, assoc.; Canada, Alberta, George Lake, 53°57′N 114°06′W, August 5, 1977, J. S. Ashe, ex *Clitocybe* sp.: *Gyrophaena* sp. (pulchella group); 7, instar III, assoc.; Canada, Alberta, George Lake, 53°57′N 114°06′W, August 11, 1977, J. S. Ashe, ex *Clitocybe* sp.: *Gyrophaena simulans* Casey; 14, instar III, assoc.; Texas, Brazos Co., College Station, November 23, 1975, J. S. Ashe, ex *Tricholoma* sp. (prob. *T. sulfureum*): *Gyrophaena* undes. sp. 1 (coniciventris group); 3, instar III, assoc.; Mexico, Chiapas, 9.0 km W San Cristóbal, hwy 190, June 29, 1979, oak-pine assoc., 2390 m elev., J. S. Ashe, ex *Cortinarius* sp.: *Gyrophaena* undes. sp. 2 (coniciventris group); 1, instar I, 2, instar III, assoc.; Arizona, Coronado Natl. For., Chiricahua Mtns., Pinery Canyon Campgrd., August 5, 1976, J. S. Ashe, ex *Russula* sp.: *Gyrophaena* (*Phaenogyra*) *strictula* Erichson; 13, all instars, assoc.; England, Ashtead Woods, Surrey, 27.5.47, ex *Lenzites*-like fungus, F. v. Emden (BMNH): *Gyrophaena* (*Phaenogyra*) *subnitens* Casey; 18, all instars, ex ovo; Canada, Alberta, George Lake, 53°57′N 114°06′W, June 12, 1980, J. S. Ashe, ex small, stemmed *Lentinus* sp.

DISCUSSION—The great taxonomic and structural diversity exhibited by adults of the genus *Gyrophaena* is reflected in the structural variation found among larvae. Therefore, immatures of this genus are the most difficult to characterize of any known gyrophaenine genus. Larvae of *Gyrophaena* are similar to those of *Phanerota* and *Eumicrota* in that they share a number of similarly derived chaetotaxic features and they have similar structures of the mala of the maxilla. They may be distinguished from these latter genera by the features listed in the key. A particularly distinctive characteristic found among larvae of the great majority of *Gyrophaena* is the moderately, but distinctly, emarginate ligula, a feature not found among known larvae of *Phanerota* and *Eumicrota*. This characteristic is less useful for distinguishing all larvae of *Gyrophaena* because the emargination of the ligula is obsolete or virtually absent in larvae of a few species. In these circumstances, a combination of ligula structure, ocellus size, position and number of denticles of the lateral face of the mala, and structure of the mala is required to correctly place these larvae in *Gyrophaena*.

Even though *Gyrophaena* is relatively difficult to characterize based on larval features, a number of characteristics were found to be stable at the species or species group level. These included relative lengths of the antennomeres and associated antennal solenidea, details of the spinose features of the mala, relative sizes of characteristic setae, structure and relative size of gland reservoir and associated gland ducts of abdominal segment VIII, structure, degree of dissection, and relative lengths of filaments of brushlike setae of tergum VIII, and relative lengths of urogomphi. Combinations of these in addition to other features may prove to be useful for characterization of larvae of species, species-group, or subgeneric-level taxa within this large and heterogeneous genus.

Almost all *Gyrophaena* larvae thus far found in association with adults or reared have been taken from fleshy gilled mushrooms. Although a few species of *Gyrophaena* are most commonly found in association with leathery gilled mushrooms or soft polypores on logs (Ashe, 1984), these are unusual among members of *Gyrophaena*, and immatures of these species have not been collected. Larval host associations presented here provide additional support for the contention of Ashe (1984) that members of *Gyrophaena* are most characteristic of fleshy gilled mushrooms though he noted that diversity of hosts within the genus is great.

Gyrophaena affinis Sahlb. larvae were first described by Rey (1886). Other *Gyrophaena* larvae described include *G. cristophera* Cameron (Paulian, 1941), *G. gentilis* Erichson (White, 1977), *G. fasciata* (White, 1977), *G. strictula* Erichson (White, 1977), and *Gyrophaena* species (Boving & Craighead, 1930). Heeger (1853) described larvae that he believed were those of *G. manca* Erichson.

However, these are not gyrophaenine larvae, and White (1977) suggested that they probably represented larvae of *Oligota*. My subsequent examination of Heeger's figures supports White's conclusion.

Late Instar Larvae of *Phanerota* Casey (Figures 82-96)

DESCRIPTION—**General**—Length of mature larva 2.1–2.9 mm. General form elongate, more or less dorsoventrally depressed, broadest at intermediate abdominal segments. Color of mature larva whitish to very light gray-brown dorsally. Microsculpture absent. Vestiture of long simple setae.

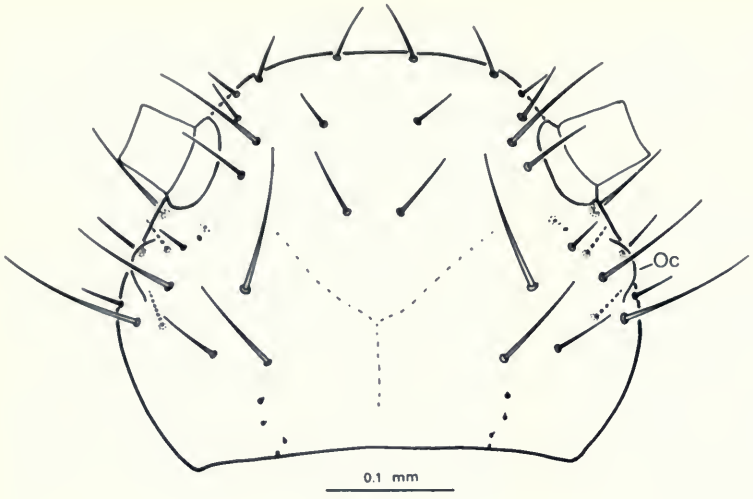
Head (Figure 82)—Length to width ratio about 0.75. Ocellus single on each side, relatively large, prominent. Ecdysial sutures very slightly developed, lateral arms not obviously attaining antennal fossae. Chaetotaxy characteristic of subtribe; campaniform sensilla Ec3 absent. Antenna as in Figure 84; 3 articled; relative lengths of articles of specimens of species available, article 1 short, 1.1 times as long as wide, article 2 1.8 times as long as 1, article 3 0.5 times as long as 2; sensory appendage on antennomere 2 elongate, spinelike, about 1.0 times length of constricted portion of article 2; antennomere 2 with solenidea IIS1 and IIS2 present, IIS3 present, minute, and spinose, IIS1 digitiform, slightly rounded at apex, about 0.33 times length of sensory appendage, IIS2, spinose, about 1.0 times as long as sensory appendage; solenidea of article 3 spinose, of similar size, not inflated or enlarged. Labrum as in Figure 86, chaetotaxy with Ld1 and Ld2 of similar size, short, setose. Epipharynx as in Figure 87. Mandibles (fig. 83) with subapical tooth small, lobe in molar area slightly developed, more distal seta of lateral basal half reduced to a pore, more proximal seta very small. Maxilla (fig. 88) typical of subtribe; mala obliquely truncate with 3–4 rows of moderately large to small teeth, teeth markedly larger distally and smaller more proximally; apex of mala with single deeply emarginate foliose scale distally; lateral surface of mala without additional scalelike teeth, lobes, or spatulate structures (fig. 89); base of adoral surface of mala with broad lobe laterally near palpus insertion and 5–6 very small microspinules near medial border (fig. 89); maxillary palpus as in Figure 88. Adoral surface of labium (hypopharynx) with numerous inwardly directed hairlike processes on each side of midline. Labium as in Figure 85; ligula short, slightly protruded, length less than length of labial palpus, truncate and slightly rounded apically, not emarginate apically, without prominent spinose or setose sensilla on each side of midline, without apical peglike sensilla, lateral surfaces without numerous hairs; labial palpus 2 articled, article 1 less than 0.5 times length of 2, apical spine slighty developed; seta near insertion of labial palpus very small.

Thorax—Pronotum (fig. 90) transverse, moderately sclerotized; chaetotaxy characteristic of subtribe; setation with discal setae Da2 and Dc2 of similar size, lateral setae L2 and L3 absent; ecdysial suture very faint. Mesonotum (fig. 91) similar to pronotum except anterior setae reduced to microtrichous pores (A2–3 absent) in slightly sclerotized anterior portion of tergum; discal setae Da2 and Dc2 present, well developed, of similar size, Dd2 absent; lateral setae L2, L3, and L5 absent. Metanotum similar to mesonotum. Legs as in Figure 93; relatively short and stocky, femur length to width ratio 2.2–2.4.

Abdomen—Abdominal terga I–VII (fig. 92) markedly transverse, anterior margin slightly sclerotized; discal setae Da2, Db3, and Dc2 present, well developed, of similar size, Da2 not in posterior row, Db3 in posterior row between P3 and P4; lateral seta L1 absent. Abdominal tergum VIII (fig. 95) markedly produced posteromedially as a broad lobe in association with well-developed tergal gland; chaetotaxy as in Figure 95, Da2 absent, Dc2 present, moderately developed; posterior seta P1 brushlike, serrations incised 0.3–0.4 times length of seta (fig. 96). Tergal gland reservoir distinct, well developed, about 0.75–1.0 times length of tergum VIII; gland ducts with loop obsolete, almost straight. Abdominal terga IX–X as in Figure 94; urogomphi single articled, about 0.5 times length of tergum X. Pseudopodium without hooks.

MATERIAL EXAMINED—*Phanerota dissimilis* (Erichson); 18, instar II–III, assoc.; Texas, Brazos Co., College Station, July 12, 1975, J. S. Ashe, ex mushrooms: *Phanerota fasciata* (Say); 13, instar III, assoc.; Texas, Brazos Co., College Station, May 31, 1975, J. S. Ashe, ex *Russula* sp.: *Phanerota fasciata* (Say); 16, all instars, reared; Texas, Brazos Co., College Station, June 2–4, 1974, J. S. Ashe, ex *Russula* sp. (prob. *R. foetans*): *Phanerota fasciata* (Say); 5, instar III, assoc.; Mississippi, Harrison Co., Big Biloxi Campgrd., 14 mi N Gulfport, VI-13-1973, on gilled mushrooms, A. Newton (MCZ).

DISCUSSION—Among gryophaenine larvae, those of *Phanerota* can be recognized by the combina-



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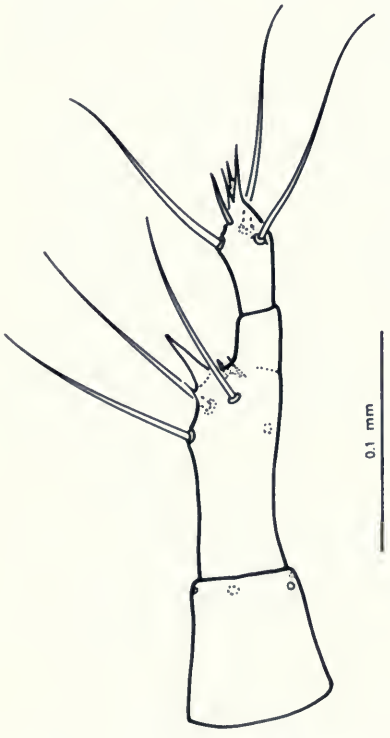

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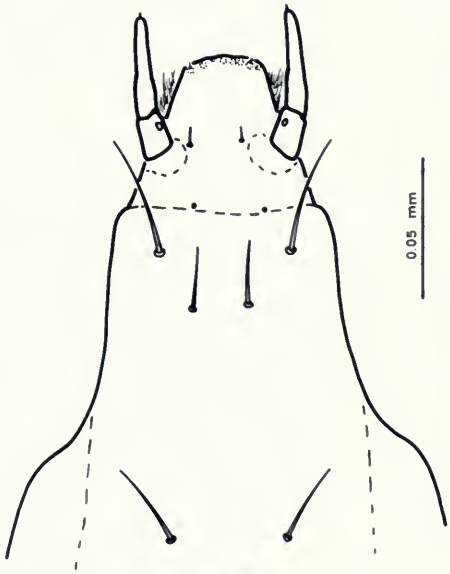

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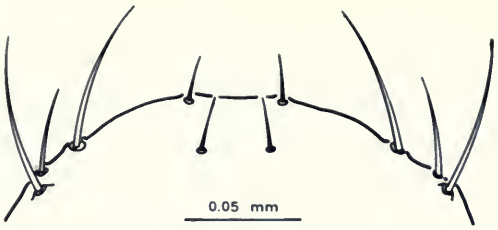
FIGS. 82–85. *Phanerota fasciata* (Say), larval instar III. **82,** Head, dorsal aspect; **83,** mandible, ventral aspect; **84,** antenna, dorsal aspect; **85,** labium, ventral aspect.



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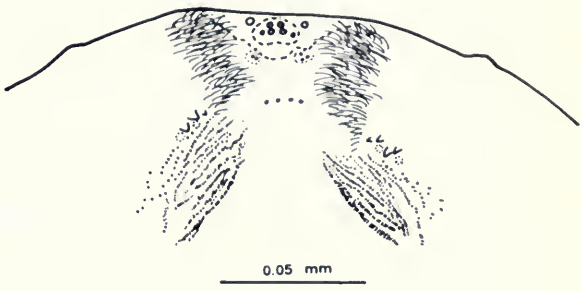

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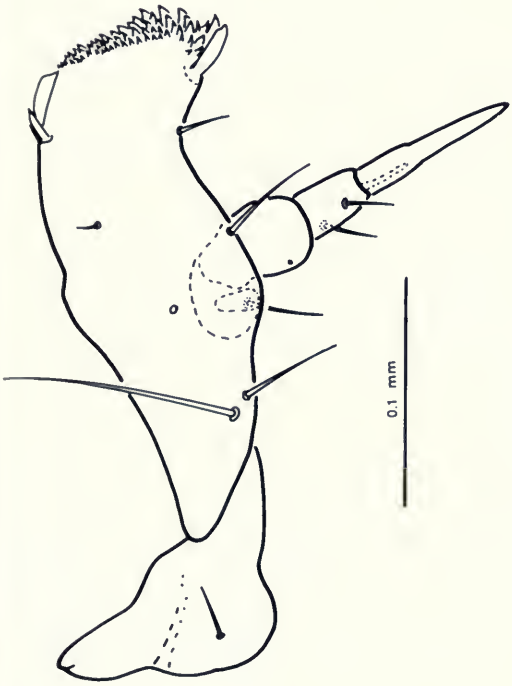

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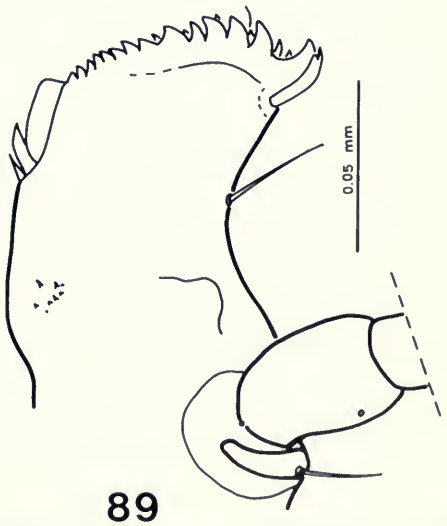

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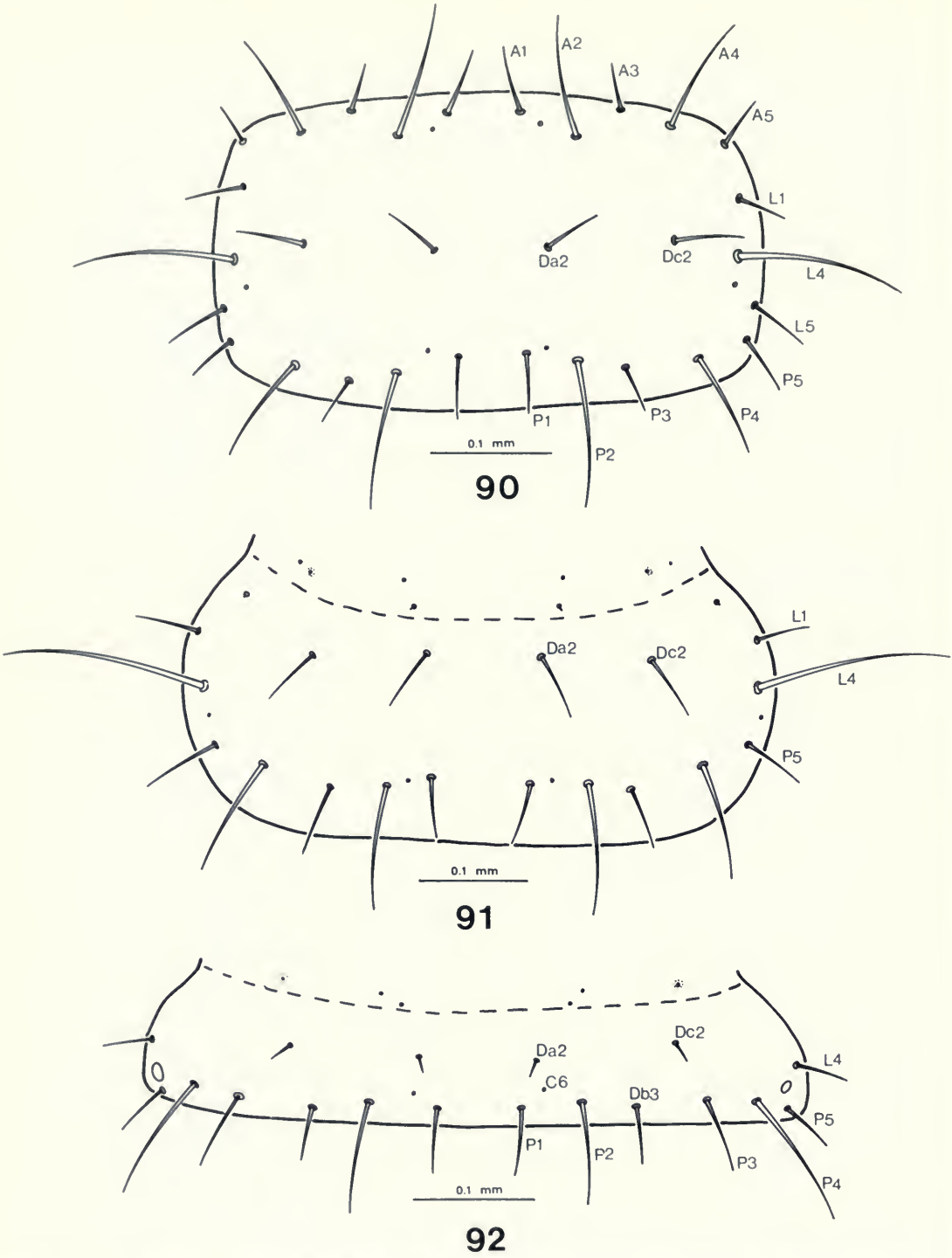
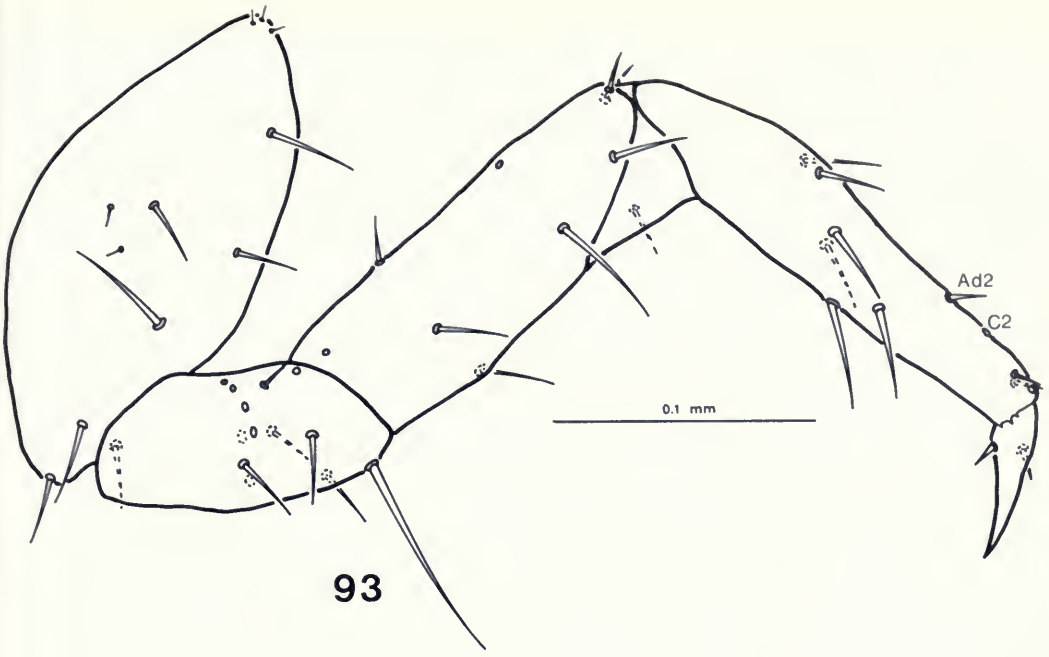
FIGS. 86–89. *Phanerota fasciata* (Say), larval instar III. **86,** Labrum, dorsal aspect; **87,** labrum, adoral aspect (epipharynx); **88,** maxilla, ventral aspect; **89,** mala of maxilla, dorsal aspect.



FIGS. 90–92. *Phanerota fasciata* (Say), larval instar III. **90,** Pronotum; **91,** mesonotum; **92,** abdominal tergum I.



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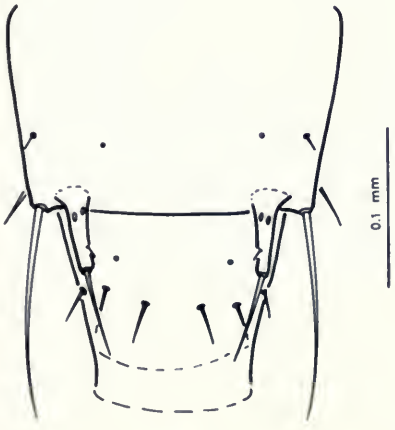

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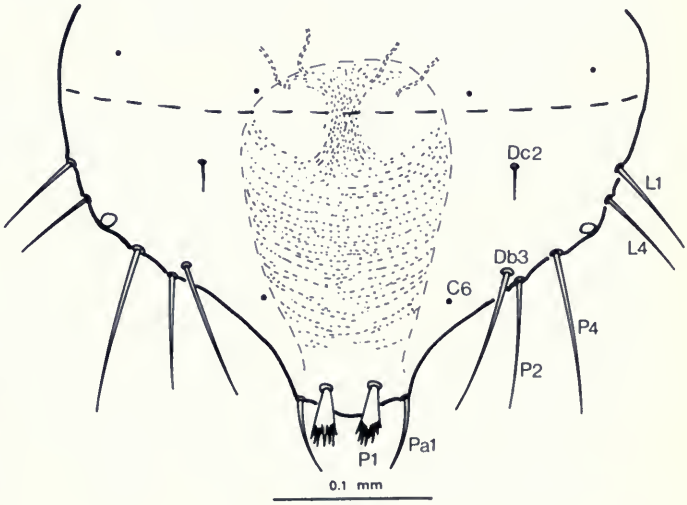

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FIGS. 93–96. *Phanerota fasciata* (Say), larval instar III. **93,** Proleg, anterior aspect; **94,** abdominal terga IX–X; **95,** abdominal tergum VIII; **96,** brushlike seta, P1 of abdominal tergum VIII, detail.

tion of the very large ocellus, truncate ligula with apical emargination, the large papillate lobe near insertion of the maxillary palpus, microspicules near proximolateral border of base on mala, and derived chaetotaxic features characteristic of other members of the "Gyrophaena" lineage (see Phylogenetic Analysis). *Phanerota* larvae are particularly distinctive for the relatively large ocelli which parallel the large, bulbous compound eyes of adults.

Larvae of *Phanerota* and *Eumicrota* share two derived features, the papillate lobe near the insertion of the maxillary palpus and the truncate ligula, and are hypothesized to be sister groups based on these characteristics. However, known adult features do not support this phylogenetic hypothesis. Instead, adult characteristics indicate a sister group relationship between *Gyrophaena* and *Phanerota* with *Eumicrota* as sister group to these two taxa. There are three possible reasons for this conflict: (1) undiscovered characteristics which would clarify relationships among these taxa are present on larvae, adults, or both; (2) parallelism has obscured homologous apotypic characters which reflect phylogeny; (3) characteristics used for phylogenetic analysis have been incorrectly analyzed. No resolution is presently possible.

Larvae of *Phanerota* have thus far been found only on species of *Russula,* and adults of *P. fasciata* (Say) breed regularly on mushrooms of this genus. Other larval-adult associations are from unidentified hosts. Ashe (1981) has discussed the host range of *P. fasciata* and (1982) that of *P. dissimilis* (Erichson) based on studies of adults.

Ashe (1981) described the development and immature stages of *Phanerota fasciata.*

Early Instar Larvae and Developmental Variation

Gyrophaenines have three larval instars, the characteristic developmental number for aleocharines. Structural differences between instars are confined primarily to chaetotaxy and are evident between the first and second instars. The second and third instars are similar in all features examined.

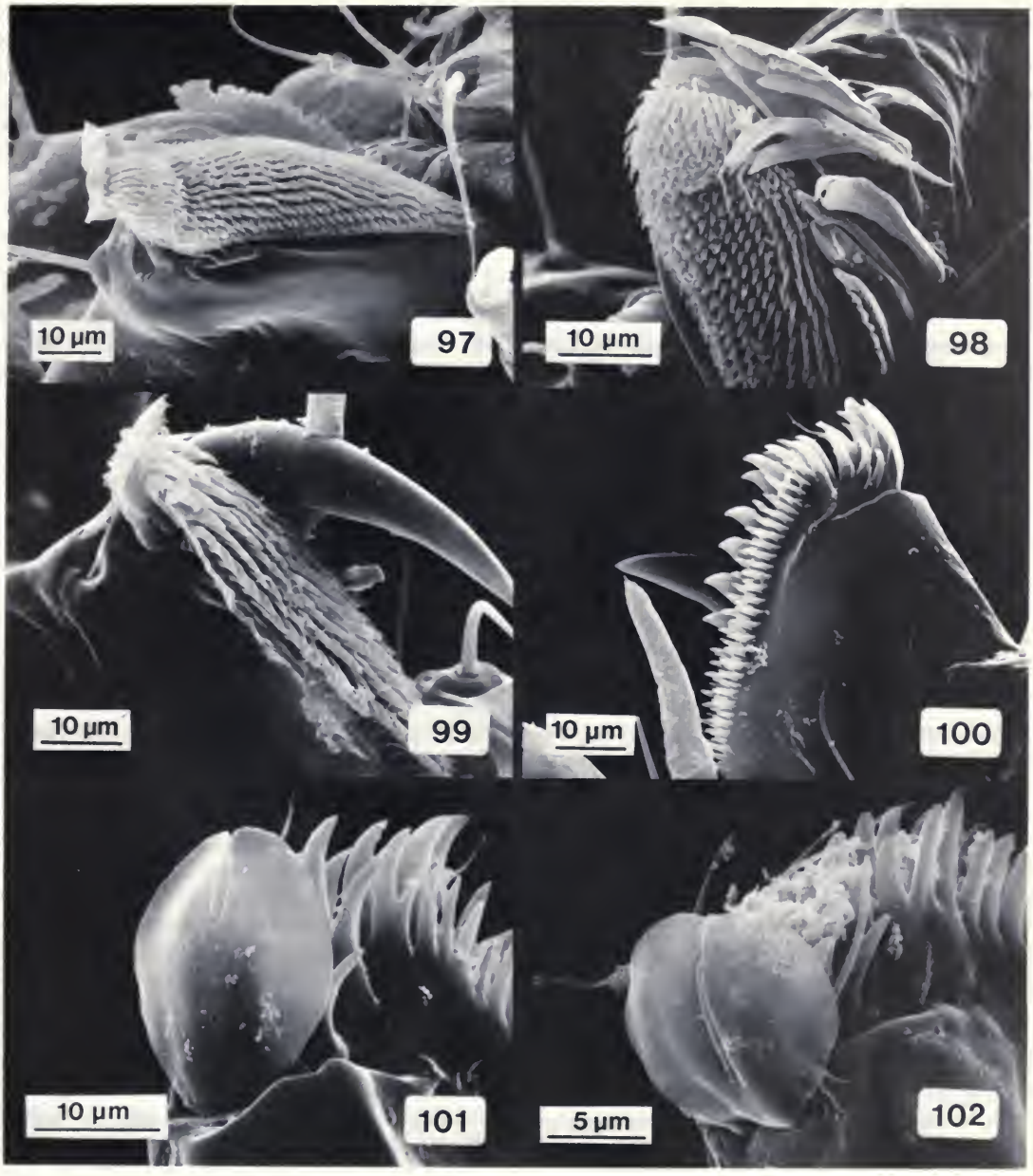
First instar larvae differ from second and third as follows: Pronotum with anterior seta A3 or both A3 and A5 absent; lateral setae L2, L3, and L5 or L3 and L5 absent; posterior seta P3 absent. Mesonotum with L5 present or absent; posterior seta P3 absent; discal seta Dd2 present or absent. Metanotum similar to mesonotum except for presence of a hatching spine on each side of midline anteromedial to Da2 and, in some, posteromedial to P1. Tarsungulus of leg noticeably longer. Abdominal terga I–VII with posterior seta P3 and discal seta Db3 absent. Abdominal tergum VIII with posterior seta P1 spatulate and serrate at apex or slightly divided into brushlike lobes distally, or setose and not at all flattened; gland reservoir of abdominal segment VIII much smaller, subglobose, more slightly sclerotized with internal loops more slightly developed.

Discussion—Many of the differences between larvae which characterize major lineages based on late instar immatures are also present in early instar larvae. For example, early instar larvae of *Agaricomorpha* and *Brachychara* have pronotal anterior seta A5 and lateral setae L2 and L5 present, whereas these are absent in first instar larvae of *Gyrophaena, Phanerota,* and *Eumicrota.* In addition, the presence on abdominal terga I–VII of Da2 in characteristic positions in the posterior row of late instar larvae of *Agaricomorpha* and *Brachychara* is also evident in first instar larvae. It is also interesting that discal seta Dd2 is present on the mesonotum of first instar larvae of *Agaricomorpha.* This seta has otherwise been found among gyrophaenines only on late instar larvae of *Agaricochara.*

Other characteristics of early instar larvae do not appear to be associated with phylogenetic lineages. Number and position of hatching spines is typical. All first instar gyrophaenine larvae have a pair of hatching spines anteromedially on the metanotum and in some (specimens of *Gyrophaena* [*Phaenogyra*] *subnitens*) also on the mesonotum. Some (specimens of *Agaricomorpha*) also have an additional smaller pair posteromedially on this tergum. Others have additional spines anteromedially on abdominal terga I or I–III (specimens of *Brachychara* and *Eumicrota*) or abdominal terga I–VI (*Gyrophaena subnitens*), with spines becoming smaller on more posterior terga.

The pattern of modification of posterior seta P1 of abdominal tergum VIII, which is brushlike or spatulate in mature larvae, is also interesting. First instar larvae of several species of *Gyrophaena* and *Agaricomorpha* have a form of these setae as simple setose setae, not at all flattened or brushlike. In other first instar *Gyrophaena, Eumicrota,* and *Phanerota* larvae these setae are narrowly spatulate and finely serrate or slightly brushlike apically, whereas those of *Brachychara* are broader and serrate at the apex.

The relatively slight development of the gland



FIGS. 97–102. SEM micrographs of maxillae of larval instar III Gyrophaenina. **97,** *Brachychara* sp. 2, apex of mala; **98,** *Brachychara* sp. 1, apex of mala; **99,** *Agaricomorpha apacheana* (Seevers), apex of mala; **100,** *Gyrophaena nana* (Paykull), apex of mala; **101,** *Gyrophaena nana* (Paykull), outer apical aspect of mala showing emarginate foliose scale; **102,** *Eumicrota corruscula* (Erichson), outer apical aspect of mala showing emarginate foliose scale.

reservoir of abdominal segment VIII is characteristic of all first instar gyrophaenine larvae examined. It is not clear whether this indicates that the gland system has a lower level of function in early instar larvae.

Ashe and Watrous (1984) pointed out that the chaetotaxy of first instar larvae is most easily interpreted as a lack of setae present on later instar larvae. They therefore based their nomenclature on late instar larvae, though they recognized that this was contrary to ontogenetic development. Studies of gyrophaenine immatures support their

decision in that the most interesting phylogenetic information appears to be found in chaetotaxy of late instar larvae. As noted above, some chaetotaxic features of early instar larvae reflect phylogenetically important features found also on later instar larvae; however, others are absent, and additional characters for phylogenetic analysis at the taxonomic level considered here do not appear to be present in first instar larvae. It seems possible that characteristics of first instar larvae may have phylogenetically important information at other levels of analysis, which have been obscured by ontogenetic development in later instar larvae. However, at present too few taxa have been comparatively studied to evaluate this supposition.

Discussion of Structural Features

In addition to larvae of the six gyrophaenine genera described here, study of immatures of over 25 additional genera along with numerous more tentatively identified or undetermined aleocharine larvae was required during the course of this study and during the previous development of a chaetotaxic system (see Ashe & Watrous, 1984). This provides the basis for a discussion of variation among gyrophaenine larvae and significant differences between these larvae and those of other aleocharines.

As noted above (see Chaetotaxy), the chaetotaxy of the cranial region of gyrophaenine larvae is significantly reduced in comparison to that of more generalized aleocharines; however, the pattern of reduction is uniform among all gyrophaenines examined. Overlaid on this basic uniformity of reduction chaetotaxic pattern are differences in detail of relative positions and development of various setae. For example, compare the relative sizes of setae Fl3 and Fm1 of larvae of *Brachychara* (fig. 31) with comparable cranial setae of specimens of other genera. Other setae show similar distinctive patterns. These differences in size and relative position are stable and provide descriptive and phylogenetic characters at various taxonomic levels, depending on group and setae concerned. The presence of campaniform sensilla Ec3 is not uniform among gyrophaenine larvae. It is present in specimens of *Agaricochara* (fig. 1), *Brachychara* (fig. 31), and *Agaricomorpha* (fig. 16) and absent in larvae of *Gyrophaena* (fig. 66), *Eumicrota* (fig. 46), and *Phanerota* (fig. 82). This distribution correlates well with other phylogenetically important characters (see below). Phylogenetically informative distribution of this sensory element graphically illustrates the value of attention to detail of chaetotaxic pattern.

In general, heads of gyrophaenine larvae are relatively short and broad. Most have length : width ratios of 0.75–0.9. This varies significantly only in larvae of *Agaricochara laevicollis* (fig. 1), which have heads which are as long as or longer than wide (length : width ratio, 1.0–1.1). White (1977) argued that larvae of *Gyrophaena* (*Phaenogyra*) *strictula* Er. and by implication other members of the subgenus *Phaenogyra* Scheerpeltz and Höfler also have quadrate or elongate heads. I was not able to confirm that this condition was characteristic of any larvae other than those of *Agaricochara laevicollis*. Larvae of *Gyrophaena* (*Phaenogyra*) *subnitens* Csy. from North America and associated larvae of *Gyrophaena* (*Phaenogyra*) *strictula* Er. from England had heads with length : width ratios within the range characteristic of members of the genus *Gyrophaena*. This, along with other characteristics, suggests that White was incorrect in placing *Gyrophaena strictula* and *Agaricochara laevicollis* together in the genus *Agaricochara* (considered a subgenus of *Gyrophaena* by him). It also further confirms the findings of Ashe (1984), based on study of adults, that *G. strictula* (and other members of the subgenus *Phaenogyra*) is actually a *Gyrophaena* and that *Gyrophaena* and *Agaricochara* should be maintained as separate genera.

White (1977) also suggested that the relatively narrow heads of both larvae and adults of *Agaricochara* were correlated with their preference for woody or leathery polypores. He suggested, based on relationships between gular sclerite size, head capsule width, and mandibular strength proposed by Evans (1964), that the narrower heads of members of *Agaricochara* would result in relatively more powerful mandibular muscles than would the wider heads of members of *Gyrophaena*. This would correlate with habits of those beetles which frequent and feed on more persistent and harder woody or leathery polypore mushrooms as opposed to the softer, fleshy gilled fungi. However, when head shape is compared among a wider range of genera and species within the Gyrophaenina, the correlation of elongate head shape with habits of feeding on woody polypores does not appear to hold true. All members of *Brachychara* and *Agaricomorpha* for which habits are known are associated only with woody polypores, yet the head proportions of larvae of *Brachychara* (fig. 31) are well within the range found among fleshy mush-

room feeding larvae of *Gyrophaena* (fig. 66), and head proportions of larvae of *Agaricomorpha* (fig. 16) are only slightly longer.

The antennae of gyrophaenine larvae are also unusual among aleocharine larvae. In particular, the spinose sensory appendage of antennomere 2 (figs. 3, 68) differs from the more globular or inflated sensory appendage found among larvae of most other aleocharines (see Topp, 1975; Ashe & Watrous, 1984). The particular combination and development of other solenidea of gyrophaenine larvae is also characteristic when compared with similar structures in other aleocharines. An additional characteristic in the antenna of gyrophaenines is the position of solenidea IIS1 and IIS2 in relation to the sensory appendage. In larvae of *Agaricomorpha* and *Brachychara,* these two solenidea are located more laterally, near the base of the sensory appendage (figs. 18, 33), rather than more ventrally and displaced from the sensory appendage as found in specimens of *Gyrophaena* (fig. 68), *Phanerota* (fig. 84), and *Eumicrota* (fig. 48). The relative sizes, position, and form of these sensory elements as well as relative lengths and widths of antennal articles, exhibit little variation among members of a species or, for some characteristics, are stable at higher taxonomic levels. This suggests that they should be useful for systematic and phylogenetic study at all levels of analysis.

Mandibular structure of gyrophaenine larvae is significantly different from that of other aleocharines. Reduction of the preapical internal tooth to a small sharp lobe in the lateroventral plane of the mandible rather than adoral and lateral and loss of serrations of the internal edge found on mandibles of most aleocharine larvae are characteristic (fig. 2). These reductions appear to be correlated with loss of the shearing, biting, and crushing function of the mandible of gyrophaenines. Mandibles of some gyrophaenines have a very slight lobe in the molar region (fig. 2), though this is absent in many (fig. 32). This lobe, however, lacks the rows of denticles found in a similar region on mandibles of adults. Such denticles in the molar region are commonly associated with fungus or spore feeding (Seevers, 1978; Ashe, 1984; Newton, 1984). Absence of such denticles on larval mandibles represents a significant difference in structure of the mouthparts of larval and adult gyrophaenines. Implications of this difference for mandibular function cannot be assessed without detailed comparative structural and functional studies. Other differences in mandibular shape, such as length and degree and angle of apical curvature (compare figs. 2 and 83), are subtle but probably significant. The structural or functional characteristics with which these differences correlate have not been determined.

An additional interesting characteristic of gyrophaenine mandibles as a group is the general reduction of the two setae on the external basal half of the mandible. These are quite large in many aleocharine larvae (see Ashe & Watrous, 1984). Among gyrophaenine larvae these two setae are small to microtrichous (fig. 2) or the more distal seta is reduced to a pore (fig. 67), and all have mandibles with the more distal seta noticeably smaller than the more basal seta.

Some of the most striking structural modifications are found in the maxillae of gyrophaenine larvae. These appear to be the primary feeding structures and exhibit remarkable structural convergences with the maxillae of adult gyrophaenines. The obliquely truncate mala covered with numerous closely spaced teeth appears to be modified for scraping maturing spores, basidia, and other hyphal structures from the hymenium of fresh mushrooms. These factors suggest that, at least in maxillary function, larvae and adult gyrophaenines are using the mushroom resource in very similar ways (Ashe, 1984). The maxillary structure of gyrophaenine larvae differs markedly from that of other aleocharine larvae. The obliquely truncate mala with more or less numerous, closely spaced teeth of gyrophaenine larvae (figs. 7, 22, 73) contrasts sharply with the more acute mala with fewer, more widely spaced teeth and spines found in most other aleocharine larvae (see Ashe & Watrous, 1984; figs. 7, 9). In addition, the spines and teeth of the mala of most gyrophaenine larvae are largest distally and smaller proximallly (fig. 73) in contrast to the opposite condition in most other aleocharines. The mala of gyrophaenine maxillae differs sufficiently from that of other aleocharines that it is difficult to establish homologies of structural features. The small to moderate blade or spine that marks the most proximal, adoral termination of the densely setose apex of the mala (fig. 73) may be homologous to the very large blade or spine of the base of the mala of most aleocharine larvae (see Topp, 1975; Ashe & Watrous, 1984). If so, it may provide a marker for establishing homologies of other structures of the gyrophaenine mala. However, this has not yet been conclusively shown.

An apparently unique feature of all larval gyrophaenine maxillae is the bifid cuplike plate on the outer apex of the mala (figs. 101–102). Ashe

(1981) first noted the presence of this structural feature in larvae of *Phanerota fasciata* (Say) and later (1984) commented on its widespread occurrence among gyrophaenine larvae. Ashe (1981) originally suggested that this platelike structure was a modified seta; however, no seta which could be homologous is known among other aleocharine larvae. This, plus the similarity of this structure to other platelike or spatulate scales found on the maxillae of some gyrophaenines (e.g., *Brachychara* sp., fig. 38) caused Ashe (1984) to suggest that this apical, bifid plate is a scalelike cuticular modification. Some doubt about the validity of this hypothesis is caused by the lack or very slight development of additional scalelike structures in many gyrophaenines (fig. 74) in which the apical plate is well developed. At present, origin and homology of this apical, bifid plate remain to be determined.

The total number, number of rows, size, and density of spines on the apex to the mala is very characteristic and uniform within taxa at a variety of levels. In general, number, density, and development of spines correlates well with phylogenetic position and host type. Members of *Gyrophaena* (fig. 73) and *Phanerota* (fig. 88), which feed exclusively on fleshy, gilled mushrooms, consistently have fewer and larger spines than members of *Agaricomorpha* (fig. 22) and *Brachychara* (fig. 37), which are found exclusively on woody or leathery polypores. Larvae of *Eumicrota* which have intermediate habits, have spines on the mala which are similar to those of *Gyrophaena* and *Phanerota* in general structure but which are much more numerous and densely arranged (figs. 52, 64). An additional interesting correlation with host preference is the tendency of larvae of those gyrophaenines which feed exclusively on woody polypores to have distal and proximal teeth more similar in size than those of larvae which feed on gilled msuhrooms (compare, respectively, figs. 7 and 73) and to have an increased number, size, and elaboration of accessory cuticular modifications associated with the apico- and dorsolateral margin of the mala (figs. 23, 38). The reason for this is not clear but may be associated with functional and structural requirements for feeding on much harder polypore mushrooms. It is interesting that similar correlations of maxillary feeding structures with host type are found among adult gyrophaenines (Ashe, 1984). This suggests that a similar selective regime is influencing these primary feeding structures in both adults and larvae.

The base of the mala of most gyrophaenines has patches of microspinules dorsolaterally on each side of the midline (figs. 8, 74). Number and position of these denticles is fairly constant within a species. Such microspinules are absent in all known larvae of *Phanerota* and *Eumicrota*. In larvae of these genera they are replaced by a distinct papillate structure laterally near the palpal insertion (fig. 53). A purpose and function for these microspinules and papillae cannot be suggested based on available information.

Functionally, gyrophaenine maxillae operate somewhat differently from those of most other aleocharines. The mala of the majority of aleocharines is adapted for grasping, manipulating, and tearing food, and the toothed malar surfaces occlude in a more or less horizontal plane. The spinose apex of the mala of gyrophaenines is in a more or less horizontal plane when open, but rotates as it is closed so that at occlusion the larger distal apex is ventral and the smaller, proximal apex is dorsal around the oral cavity. In occluded position, the flattened, morphologically ventral surface is adoral and the mala assumes a more or less vertical position with the apex and spines of the mala angled slightly to moderately inward. In full repose, the spines of opposite maxillae may interdigitate. Additionally, in this position, the larger spines, scales, and spatulate structures on the dorsoapical side of the mala which are characteristic of some gyrophaenine larvae (fig. 98) form the lateral margins of the oral cavity. These structural and functional characteristics suggest that the malar regions of maxillae of gyrophaenines are acting as combs and scoops to remove food material from the hymenium of mushrooms and transfer it to the buccal cavity.

The broad, truncate ligula of gyrophaenines is typically shorter than the two articled labial palpi and is distinctive in comparison to the more common elongate ligula of athetine, most bolitocharine, and most oxypodine larvae (see Topp, 1975, figs. 2, 29; Ashe & Watrous, 1984, fig. 8). However, broad, truncate ligulae are not limited to the Gyrophaenina (personal observations). The short, truncate gyrophaenine ligula may be deeply (fig. 19), moderately (fig. 69), or not emarginate (fig. 85) and is characteristic at the generic level among most known larvae. More intrageneric variability in this structure is found among species of *Gyrophaena* in which the ligula varies from moderately emarginate in larvae of most species to not emarginate in larvae of a few species. In addition to shape of the ligula, distribution of sensory elements on the ligula is distinctive at the generic or

higher level. The prominent, setose sensilla found on the ligulae of larvae of *Brachychara* (fig. 34) and *Agaricomorpha* (fig. 19) are absent from those of other gyrophaenines. However, the small spinose sensory structures of the ligula of larvae of *Agaricochara* (fig. 4) may be homologous to these setose sensilla. The remarkable development of spinose sensory elements on the apex of the ligula in larvae of *Eumicrota cornuta* Casey (fig. 63) has not been observed among other gyrophaenines. Preliminary observations suggest that distribution and detailed development of other sensory elements may provide characters for use in systematic and phylogenetic studies at a number of taxonomic levels.

Legs of gyrophaenine larvae differ among specimens of different genera in several ways. Larvae of *Brachychara* (fig. 42) and *Agaricomorpha* (fig. 27) have legs which are noticeably longer and more slender than the shorter and more robust legs of immatures of *Gyrophaena* (fig. 77), *Eumicrota* (fig. 54), and *Phanerota* (fig. 93). This is reflected in the length : width ratios of the femur (see appropriate description), but also in the proportions of the other leg segments, and is particularly noticeable in the long slender tarsungulus of larvae of *Brachychara* (fig. 42). Legs of *Agaricochara* larvae (fig. 12) are more or less between these extremes. Distribution of these general leg forms correlates both with phylogenetic position and host preference. It is tempting to suggest that differences in leg proportions reflect differing requirements for living on polypore or gilled mushrooms. However, it does not seem possible to evaluate which is the more plesiotypic condition at present.

In addition to this difference, legs of larvae of *Gyrophaena* (fig. 77), *Eumicrota* (fig. 54), and *Phanerota* (fig. 93) have the campaniform sensilla C2 of the tibia distal to seta Ad2 as opposed to proximal to this seta as in legs of larvae of *Brachychara* (fig. 42) and *Agaricomorpha* (fig. 27). Larvae of *Agaricochara* have the condition of this character similar to these latter two genera though the campaniform sensilla is much closer to the seta. Since it is not presently possible to analyze polarity of states of this character, it is not possible to evaluate phylogenetic information available. However, distribution of these states correlates well with phylogenetic groupings based on other characters.

Thoracic and abdominal terga are characterized by a distinctive reduced chaetotaxy (see Chaetotaxy above) which is particularly striking in the reduction of setae in the discal rows. In general, setae present on these terga are more or less uniform among gyrophaenine larvae examined. Larvae of *Agaricochara* differ from all others in the presence of a seta interpreted as Dd2 on the mesonotum, metanotum, and abdominal terga I–VII. Also of particular interest is the presence of Da2 in the posterior row of setae of abdominal terga of larvae of *Brachychara* (fig. 41) and *Agaricomorpha* (fig. 26). Though this condition is limited to members of these two groups, which are hypothesized to be sister groups on the basis of other characters, position of this seta may not be homologous in these two genera. This conclusion is a result of the fact that Da2 occurs on opposite sides of campaniform sensilla C6 in larvae of *Brachychara* and *Agaricomorpha*. It is not clear whether the position of Da2 in relation to this sensilla or the position of Da2 in the posterior row is the more fundamental condition. The latter has been tentatively accepted in this study pending further studies.

Abdominal tergum VIII of gyrophaenine larvae is especially prominent because of the large mediodorsal and posterior lobe of this tergum associated with a very well-developed tergal gland and gland reservoir (figs. 13, 29). The gland reservoir of gyrophaenines is as large or larger than the tergum in most and is moderately darkened and strengthened by a distinctive pattern of looplike sclerotized supports (fig. 59). The four gland ducts that enter the gland anteriorly are sclerotized tubes in all gyrophaenine larvae. These gland ducts are singly looped in most (fig. 59); however, in larvae of *Phanerota* (fig. 95) the loop is obsolete and gland ducts are almost straight, and larvae of *Agaricochara* have a second loop slightly to moderately developed. Though details vary in different groups, this general type of tergum VIII glandular system is similar to that found among larvae of most Bolitocharini, Phytosini, and Myllaenini among others. It is significantly different from that of most Athetini and Oxypodini. Larvae of these latter groups have an eighth abdominal tergum in which presence of a tergal gland and reservoir does not have a noticeable external manifestation and which have, at most, only slightly sclerotized to completely membranous gland reservoirs and usually a different structure of sclerotized portions of the gland ducts (see Ashe & Watrous, 1984, fig. 22).

A unique feature of gyrophaenine larvae, as far as is known, is the modification of posterior seta P1 of abdominal tergum VIII into brushlike setae. First described by White (1977) in larvae of *Gyrophaena gentilis* Er. and later by Ashe (1981) in

larvae of *Phanerota fasciata* (Say), they were noted to be present in all gyrophaenine larvae examined by Ashe (1984). Examination of numerous additional gyrophaenine and other aleocharine larvae during this study has further supported this latter assertion and provided confirmation of the unique nature of these brushlike setae among aleocharine larvae. Detailed structure of these setae varies considerably among genera and species. Those of *Agaricochara* (fig. 14) and *Agaricomorpha* (fig. 30) are the least brushlike and are only flattened, spatulate, and finely serrate apically rather than deeply divided into filiform lobes. Those of *Brachychara* (fig. 44) are broadest and are divided into the greatest number of these setose lobes of any known gyrophaenine, whereas the brushlike setae of most larvae of *Gyrophaena* (fig. 81) are deeply divided into a few very long filiform processes. Brushlike setae of larvae of *Phanerota* (fig. 96) and *Eumicrota* (fig. 61) are between these extremes of width and degree of apical dissection. Although there is some variation of detailed form of brushlike setae among specimens within a species, the general structure of these setae is often characteristic of species, species-group, or genus-level taxa. Ashe (1981) suggested that these setae were probably modified from typical setae in similar positions in other aleocharine larvae; however, he was not aware of such plesiotypic homologous setae at that time. Typical, well-developed setae have since been found in relatively homologus positions of brushlike setae on the median apex of the tergal gland lobe of larvae of several *Bolitochara* species, *Leptusa* species, and several other aleocharines (personal observations). These setae are almost certainly homologous primitive states of brushlike setae on gyrophaenine larvae. No hypothesis about importance or function of brushlike setae or why they are limited to gyrophaenines can be suggested until more detailed behavioral and ecological observations are available.

I interpret the urogomphi of all typical Aleocharinae as single articled. This appears to be true even in those larvae in which the articulated urogomphus is small and displaced from the tergum by a considerable unarticulated lobe (as in larvae of *Agaricomorpha* [fig. 28]). Though this unarticulated lobe may become very long and the articulated urogomphus quite short in some aleocharine larvae (personal observations), it seems most consistent to consider this lobe to be simply an elongation of the posterolateral margins of tergum IX. In all aleocharine larvae examined the base of the articulated urogomphus can be recognized by the presence of two distinct oblong campaniform sensillae (e.g., figs. 15, 58). Under these criteria, all gyrophaenine larvae have single-articulated urogomphi. Urogomphi differ among gyrophaenine larvae primarily in the length of the urogomphus relative to tergum IX. Among late instar larvae, the relatively shortest urogomphi are found among specimens of *Brachychara* (fig. 45), and the longest are among specimens of *Agaricomorpha* (fig. 28). The relative lengths of other gyrophaenine urogomphi fall between these extremes.

Most aleocharine larvae have four large, well-developed hooks on the pseudopod. These are absent from known larvae of all gyrophaenines. The relationship of absence of these hooks to obligatory association with fresh mushrooms cannot be evaluated at present. However, it is interesting that though larvae of *Bolitochara* have these hooks, they are much smaller than those of most other aleocharines. Adults and larvae of *Bolitochara* also have an association with fresh mushrooms, though it is apparently not as obligatory as that of gyrophaenines (Topp, 1973; Ashe, 1984).

Phylogenetic Analysis

Character Analysis

The procedure used in analysis of relationships of taxa in this study is based on the methods and principals of phylogenetic analysis or cladism of Hennig (1965, 1966) and are consistent with those used by Ashe (1984) in study of adult gyrophaenines.

One of the most fundamental processes in this method is analysis of characters. The primary steps in this procedure are recognition and description of homologous characters and determination of primitive (plesiotypic) and derived (apotypic) states of these characters. These critical steps present particularly serious problems in study of any group of larval aleocharines because of the very limited knowledge of these larvae in general, and, subsequently, inadequate understanding of distribution of character states at all taxonomic levels. Other than very preliminary discussions of distribution of characteristics associated with the tergal gland of abdominal segment VIII (Moore, 1978; Frank & Thomas, 1984), there has been no serious attempt to provide phylogenetically meaningful analyses of characteristics of aleocharine larvae.

TABLE 1. Plesiotypic and apotypic states of characters used in phylogenetic analysis of gyrophaenine larvae.

Character	Plesiotypic	Apotypic
HEAD		
1. Setae	All typical setae present	Head setae reduced (El1, Em2–3, Vl1–3, V1 absent)
2. Campaniform sensillae	All typical sensillae present	All absent except Ec1 and Ec3
3. Campaniform sensillae	Ec1 and Ec3 present	Ec3 absent
OCELLUS		
4. Size	Small	Large
MANDIBLE		
5. Teeth	Inner edge serrate	Inner edge not serrate
6. Inner tooth	Prominent, in horizontal plane of mandible	Small, in lateroventral plane of mandible
7. External setae	Both external setae large to moderate, prominent, similarly sized	Both external setae small, more distal seta often smaller than proximal seta
8. External setae	Both distal and proximal present	Distal seta reduced to a pore
MAXILLA		
9. Mala	Apex more or less acute	Apex obliquely truncate
10. Mala	With dispersed shearing plates, teeth, and spines	With numerous densely arranged spines and teeth
11. Mala	Without emarginate leaflike scale externally	With emarginate leaflike scale externally
12. Mala	Accessory scales of distolateral face simple, toothlike	Accessory scales of distolateral face complex, foliose, spatulate, or spinose
13. Mala	Spinose area not raised into accessory lobe distally	Spinose area distinctly raised into accessory lobe distally
14. Mala	Without papillus or broad lobe basolaterally near palpal insertion	With papillus or broad lobe basolaterally near palpal insertion
LABIUM		
15. Ligula	Elongate, longer than wide	Short, stout
16. Ligula	Apex emarginate	Apex entire, truncate
17. Ligula	Without distinct setose sensilla on side of midline near apex	With distinct setose sensilla on each side of midline near apex
18. Seta	Seta near palpal insertion large	Seta near palpal insertion moderate sized or small
19. Seta	Seta near palpal insertion moderate sized	Seta near palpal insertion small to very small
20. Palpus: apical sensilla	Very small	Moderately large, prominent
ANTENNA		
21. Sensory appendage	Inflated	Spinelike
22. Solenidea	IIS3 present, moderate in size	IIS3 very small or absent
23. Solenidea	IIS1 and IIS2 more or less similar in size (within 50% or more)	IIS2 very small in comparison to IIS1 (less than 50%)
PROTHORAX		
24. Discal setae	Discal rows complete	Only Da2 and Dc2 present
25. Lateral setae	Lateral rows complete	Lateral setae L2 and L3 absent
26. Discal setae	Da2 and Dc2 similar in size, or Dc2 only slightly larger	Dc2 distinctly larger than Da2
27. Campaniform sensillae	Sensillae C1–6 present in each half	Only C1, C3, and C6 present

Continued on next page

TABLE 1. *Continued.*

Character	Plesiotypic	Apotypic
MESOTHORAX		
28. Discal setae	Da2–3, Db1–3, Dc2, and Dd2 present	Only Da2, Dc2, and in some, Dd2 present
29. Discal setae	Da2 and Dc2 similar in size	Dc2 much larger than Da2
30. Campaniform sensillae	Sensilla C4 present	Sensilla C4 absent
ABDOMINAL TERGUM		
31. I: setae	Discal seta Da2 not in posterior row	Discal seta Da2 in posterior row
32. VIII: gland	Gland ducts present as singly or doubly looped sclerotized tubes	Gland duct loops obsolete
33. VIII: setae	Posterior seta P1 setose	Posterior seta P1 spatulate or brushlike
34. VIII: setae	Posterior seta P1 spatulate	Posterior seta P1 brushlike

Although a relatively large number of aleocharine larvae representing a diversity of higher taxa were examined in the course of this study, compared with overall diversity of the Aleocharinae, such a survey must be relatively superficial. Because of this, it seems likely that the details of character analysis presented here, and, consequently, the phylogenetic hypotheses developed, may require modification with increased knowledge. In addition, comparison of other gyrophaenine and aleocharine larvae will reveal a number of additional characteristics, not considered in detail here, which are almost certainly useful for systematic or phylogentic studies but which cannot be properly analyzed at this time. It is hoped that the analysis of characters presented here will serve as a stimulus and a starting place for such additional studies.

Methods of analysis of characters in this study involved both comparison of states of homologous characters among members of the groups being studied (in-group comparisons) and comparisons among closely and more distantly related taxa (out-group comparisons) (see Watrous & Wheeler, 1981, for discussion). Larvae of species-level and higher taxa of the Gyrophaenina provided in-group comparisons. Out-group comparisons from a relatively closely related group were provided by study of larvae of the subtribe Bolitocharina, including reared larvae of *Bolitochara lunulata* Payk. and *Leptusa ruficollis* Er. and associated larvae of *Bolitochara* species, *Leptusa* species, *Amonognathus* species, *Homalota* species, and *Placusa despecta* Er. Out-group comparisons from more distantly removed aleocharines were provided by identified or associated larvae of several genera each in the Athetini, Oxypodini, Tachyusini, Phytosini, Myrmedonini (sensu Seevers, 1978), and other determined and numerous undetermined aleocharine larvae. In general, it is here argued that character states restricted to the Gyrophaenina or states which are relatively more restricted among gyrophaenines and other aleocharines are derived. In contrast, states found in some but not all gyrophaenines in addition to bolitocharines and other aleocharines are relatively plesiotypic. However, because of the complex nature of many of the character systems, each character must be analyzed separately and compared with others for congruence.

Table 1 summarizes the plesiotypic and apotypic character states used in reconstruction of phylogenetic relationships in this study.

The general trend of reduction in many characteristics of gyrophaenine larvae, particularly those involving chaetotaxic patterns, presents difficulty in interpretation of homologous apotypic states. This primarily results from the fact that losses and reductions may reach identical ends by different and nonhomologous pathways (Hecht & Edwards, 1977). However, the concordance in a variety of chaetotaxic characters among all known gyrophaenines is impressive and lends strong support for the hypothesis that such chaetotaxic patterns are homologous within these taxa. For this reason, I have treated distinctive reduced chaetotaxic patterns (e.g., chaetotaxy of the head) as a single character state even though it actually represents a character complex which, however, cannot be further analyzed at present.

The distribution of plesiotypic and apotypic character states for 34 characters among larvae of gyrophaenine genera is given in Table 2. In this table plesiotypic states are scored "0," while apotypic states are "1."

TABLE 2. Distribution of binary coded plesiotypic (0) and apotypic (1) states of 34 character systems among late instar larvae of gyrophaenine genera and the subtribe Bolitocharina.

Larvae	1-5	6-10	11-15	16-20	21-25	26-30	31-34
Agaricochara	11001	11011	11001	00100	11010	01100	0010
Agaricomorpha	11001	11111	11001	01101	11110	01101	1010
Brachychara	11001	11011	11101	01001	11110	11111	1011
Eumicrota	11101	11111	10011	10110	11011	01101	0011
Gyrophaena	11101	11111	10001	00110	11011	01101	0011
Phanerota	11111	11111	10011	10110	11011	01101	0111
Bolitocharina	00000	00000	00000	00000	00000	00000	0100

Cladistic Relationships

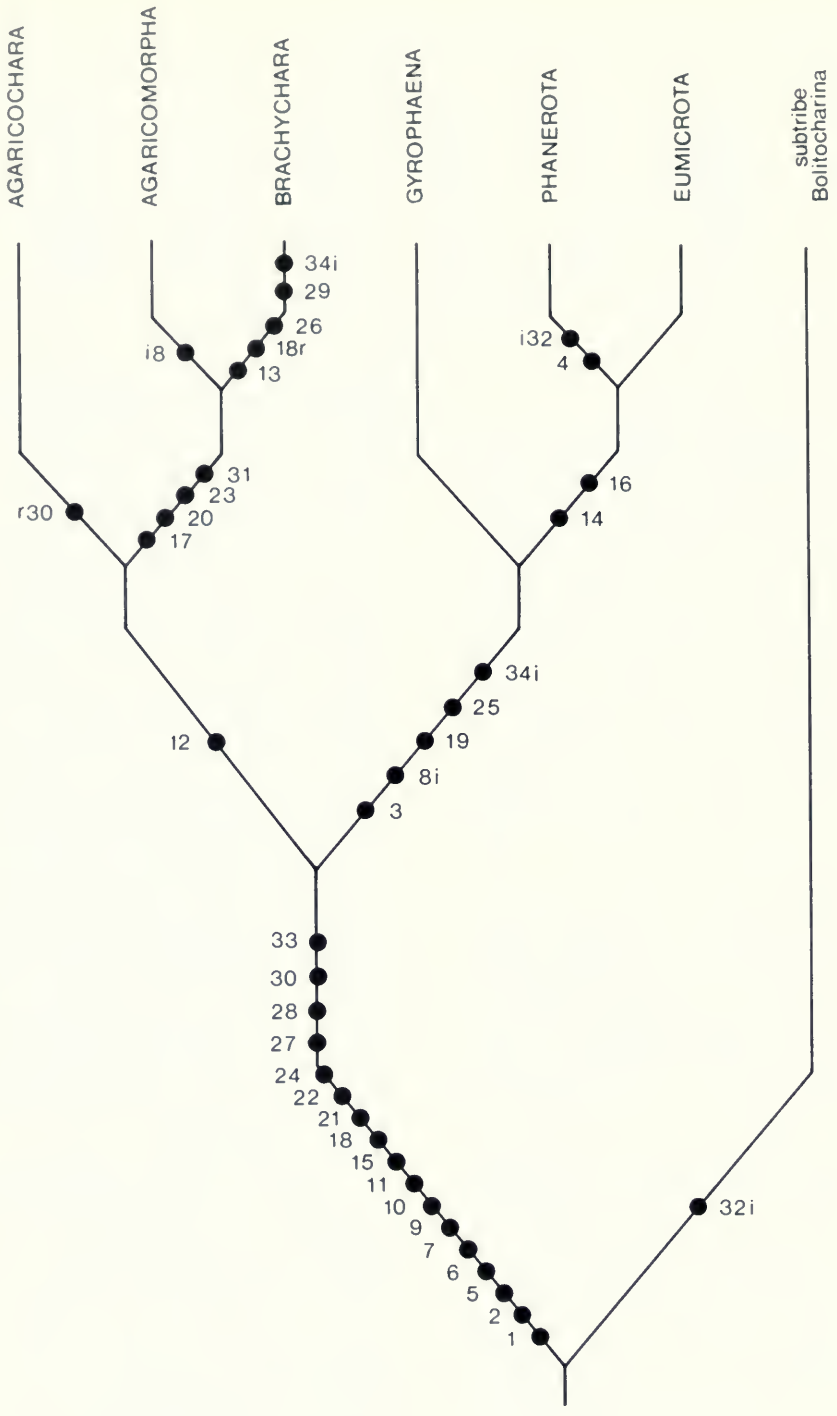
Cladistic analysis of taxa of gyrophaenines based on larval characteristics was aided by use of a phylogenetic tree reconstruction program, entitled "QTREE" written by L. E. Watrous and run on a PDP 11-40 computer. This program is based on the Wagner tree algorithm described by Ferris (1970; L. E. Watrous, personal communication). Options included in the program and used in the analysis include sorting of and addition of taxa to the tree both by randomization and by increasing or decreasing difference from starting taxon and optimization of higher taxonomic unit after each operational taxonomic unit is added. Cladograms formed by this program were compared with those produced by hand-worked traditional cladistic methods and found to be equivalent.

The minimum number of steps for reconstruction of the most parsimonius tree with these data is 39. At this number of steps there are two equally probable trees. These are presented in Figures 103 and 104 and are designated Hypothesis I and II, respectively. These hypotheses of relationship differ primarily in the position of *Agaricochara* on the cladogram and subsequent distribution of derived character states.

Analysis of relationships of members of the subtribe Bolitocharina included herein do not provide strong support for the hypothesis that the Bolitocharina are monophyletic in relation to the Gyrophaenina. The primary reason for including this group is to provide a comparative base among more typical aleocharine larvae for the distribution of apotypic character states among gyrophaenine larvae. It further serves to emphasize the highly autapotypic nature of the Gyrophaenina as a whole.

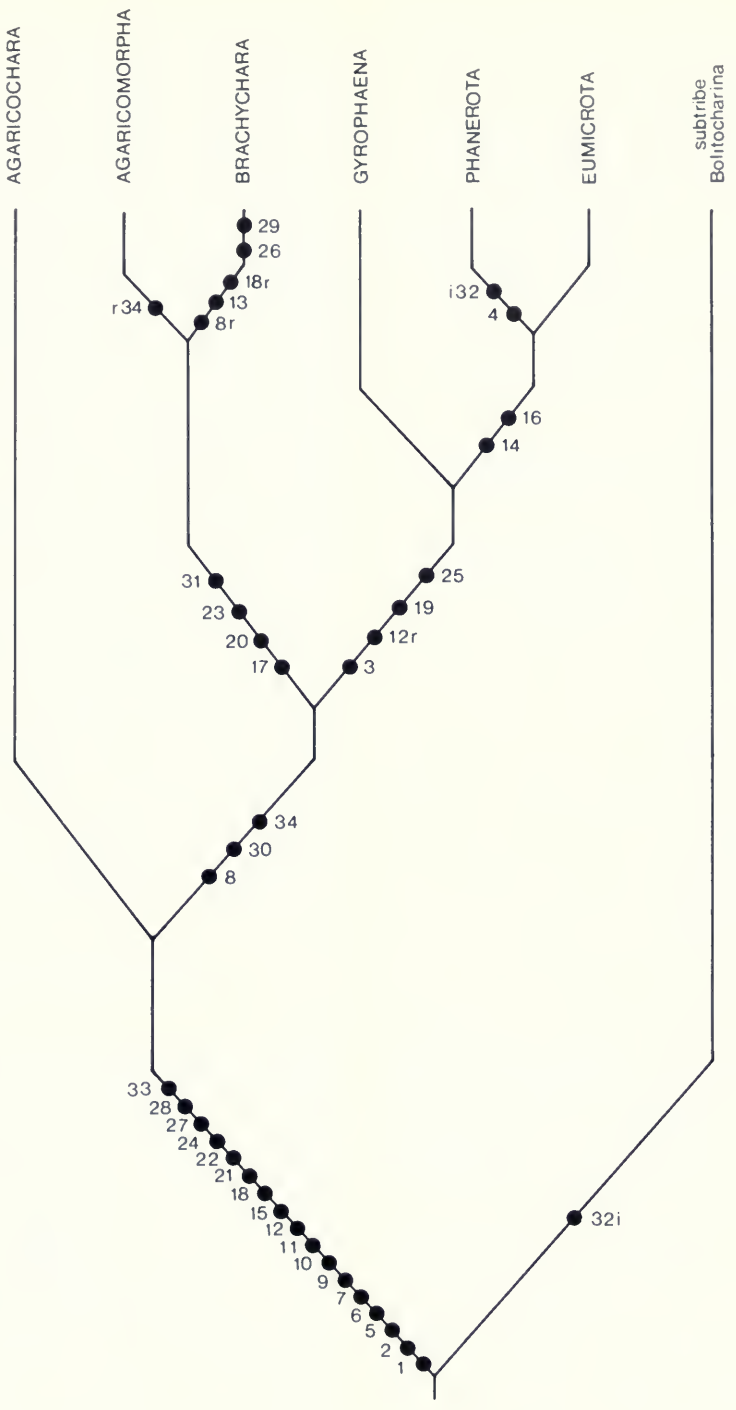
Larvae of the subtribe Bolitocharina (sensu Seevers, 1978), especially those of *Bolitochara* and *Leptusa,* share a number of characteristics with gyrophaenine larvae. These include (1) similar structure of the eighth tergal gland reservoir; (2) similar structure of the sclerotized tubular gland ducts; (3) a pair of setae (P1) in the medioapical position of abdominal tergum VIII which are probably homologous to the brushlike setae of gyrophaenines; (4) elongate, rather than bladelike, spine at base of inner edge of the mala (assumes that this spine in gyrophaenine larvae is homologous to that of bolitocharines); and (5) reduced anal hooks (absent in gyrophaenines). However, except for reduction of anal hooks, there is no evidence that suggests that these are apotypic rather than plesiotypic characteristics. Therefore, based on larval characteristics, the hypothesis that the subtribe Bolitocharina forms the sister group to the Gyrophaenina, which was developed by Ashe (1984) based on adult characteristics, is not given substantial additional support. However, no known characteristics of bolitocharine larvae suggest that this hypothesis should be refuted. The problem of sister group relationships among these taxa requires further study. Gyrophaenine larvae do not share concordant apotypic characteristics with any other group of aleocharines as far as is known. In addition, they lack many of the specialized features of larvae of the Athetini, Oxypodini, Myrmedonini, and others.

Gyrophaenine larvae occupy a structurally relatively isolated position among aleocharine larvae because of the large complex of concordant apotypic character states found uniquely among all gyrophaenines. Both Hypothesis I and II indicate that the Gyrophaenina is a monophyletic assemblage based on a total of 17 apotypic characteristics. Many of these are represented by apotypic states which involve reductions. Table 3 compares the character states which involve losses or reductions with those that involve gains of new structures. Synapotypic character states shared by all known gyrophaenine larvae which involve gains are highly concordant with synapotypic states which involve losses. This adds considerable sup-



103

FIG. 103. Cladistic relationships among genera of Gyrophaenina based on larval characteristics: Hypothesis I. Abbreviations: i, independent evolution; r, reversal.



104

FIG. 104. Cladistic relationships among genera of Gyrophaenina based on larval characteristics: Hypothesis II. Abbreviations: i, independent evolution; r, reversal.

TABLE 3. Comparisons of losses or reductions and gains among uniquely derived characters shared by all known larvae of Gyrophaenina.

Losses or reductions	Gains
Head setae characteristically reduced (char. 1)	Apex of mala obliquely truncate (char. 9)
All head campaniform sensillae absent except Ec1 and Ec3 (char. 2)	Mala with numerous, densely arranged spines and teeth (char. 10)
Inner edge of mandible not serrate (char. 5)	Mala with emarginate leaflike scale apically (char. 11)
Subapical tooth of mandible small, in latero-ventral plane of mandible (char. 6)	Ligula short and stout (char. 15)
Both external setae in basal half of mandible small (char. 7)	Sensory appendage of antenna spinelike (char. 21)
Seta on labium near base of palpal insertion moderate to small (char. 18)	Posterior seta P1 of abdominal tergum VIII spatulate or brushlike (char. 33)
Solenidium IIS3 of antenna very small, minute, or absent (char. 22)	...
Discal setae of pronotum characteristically reduced (char. 24)	...
Pronotal campaniform sensillae C2, C4, and C5 absent (char. 27)	...
Mesothoracic discal setae reduced to Da2, Dc2, and Dd2 (char. 28)	...

port to the hypothesis that those character states which involve losses are uniquely derived and therefore homologous within the Gyrophaenina.

As noted above, this large number of apotypic character states and their uniformly concordant nature firmly supports the hypothesis that the Gyrophaenina is of monophyletic origin.

Among the most parsimonious hypotheses available, Hypothesis I and II differ primarily in that Hypothesis I divides the Gyrophaenina into two major lineages with *Agaricochara* as the sister group of *Agaricomorpha* + *Brachychara*. In contrast, Hypothesis II places *Agaricochara* as the sister group to all other available gyrophaenine higher taxa. The two hypotheses are similar in that, in both, the *Agaricomorpha* + *Brachychara* lineage and the *Gyrophaena* + *Phanerota* + *Eumicrota* lineage are well supported by corroborated and strong apotypies. The character states that support these lineages are identical in both cladograms for the *Agaricomorpha* + *Brachychara* lineage, but both the characters and total number of apotypies supporting the *Gyrophaena* + *Phanerota* + *Eumicrota* lineage differ. However, characters 3 and 19 are uniform in support of the monophyly of this lineage in both cladograms. Also similar in both hypotheses, *Gyrophaena* is hypothesized to be the sister group of *Phanerota* + *Eumicrota* which are, in turn, sister groups based on shared apotypies of characters 14 and 16. In both cladograms *Gyrophaena* lacks autapotypic characters which would demonstrate the monophyletic nature of this lineage in comparison to *Phanerota* + *Eumicrota*. Therefore, the hypothesis that *Gyrophaena* is paraphyletic in relation to these genera cannot be refuted. However, the paraphyletic nature of *Gyrophaena* must be demonstrated by showing that other genera are derived from some taxon presently included in *Gyrophaena*. This has not yet been done. Similarly, *Eumicrota* cannot be presently shown to be monophyletic based on available larval characters. In both of these instances of possible paraphyly, analysis of additional characters in a wider variety of gyrophaenine larvae and increased understanding of character distributions in aleocharine larvae as a whole may provide the information necessary for unambiguous support for monophyly or paraphyly.

Hypothesis I (fig. 103) places *Agaricochara* as sister group to the *Agaricomorpha* + *Brachychara* lineage based on shared possession of the apotypic state of only a single character (character 12). Apotypic states of this character are defined by enhancement of the accessory scales, plates, and spines of the distolateral side of the mala. As noted above (see Structural Features), such structures are strongly correlated with the habit of feeding on hard, woody mushrooms. Because of this, and without additional concordant apotypic characters, evidence for monophyly of this lineage (including *Agaricochara*) must be suspect. If, however, Hypothesis I is accepted, interpretation of the distribution of character states requires that reduction of the distal seta of the lateral base of the mandible (character 8) has occurred independently in *Agaricochara* and the ancestor of the *Gyrophaena* + *Phanerota* + *Eumicrota* lineage. In addition, independent evolution of deeply divided brushlike setae on abdominal tergum VIII must have occurred in the ancestor of the latter lineage and *Brachychara*. The possibility of this latter independent evolution of apotypic character states is supported by the number of strong apo-

typies which indicate a sister group relationship between *Agaricomorpha* and *Brachychara.*

Hypothesis II (fig. 104) differs in that it hypothesizes that *Agaricochara* is the sister group of all other available gyrophaenine taxa. Under this hypothesis *Agaricochara* cannot be demonstrated to be monophyletic in relation to the remainder of the Gyrophaenina based on available larval characters; however, the remainder of the Gyrophaenina are hypothesized to be monophyletic based on the shared presence of three apotypic character states. This hypothesis requires reversals in characters 8, 12, 18, and 34. However, under the algorithm used, interpretation of reversals as independent evolution of apotypic states in other lineages of the tree is equally valid. For example, in Hypothesis II, characters 8 and 34 could be considered synapotypic for the *Gyrophaena* + *Phanerota* + *Eumicrota* lineage, with apotypic states of character 8 independently derived in *Agaricochara* and 34 independently derived in *Brachychara.* Similarly, character 12 could be considered independently derived for the *Agaricomorpha* + *Brachychara* lineage and would thereby be shared with *Agaricochara.* In this instance, the cladogram of Hypothesis II becomes very similar to that of Hypothesis I. The only remaining point of contention between the two is whether the apotypic state of character 30 is derived only once or whether it is represented by a reversal to the plesiotypic condition as indicated in Hypothesis I.

Comparison with Cladistic Analysis Based on Adults

The cladistic relationships of gyrophaenine genera hypothesized here based on larval characteristics were developed independently of any preconceived concepts of relationships. However, the degree of concordance with phylogenetic relationships based on features of adults developed by using traditional cladistic techniques by Ashe (1984) is striking. Ashe (1984) recognized three major lineages of gyrophaenines: (1) a "*Brachida*" lineage (the most plesiotypic in mouthpart structure and the sister group to all other gyrophaenines), (2) a "*Sternotropa*" lineage, and (3) a "*Gyrophaena*" lineage. Of these, the latter two lineages were sister groups based on a number of strong, well-corroborated apotypies. Unfortunately, larvae of the "*Brachida*" lineage and of many genera of the "*Sternotropa*" lineage are not known. This makes cladistic analyses based on larval and adult character systems somewhat less comparable though still informative.

Cladistic analyses based on larval or adult gyrophaenines are concordant in that the "Gyrophaena" and "Sternotropa" lineages are recognizable in each. In addition, the generic composition of each of these lineages is similar in both cladograms, even though several genera are not represented by larval material.

The discrepancy in position of *Agaricochara* based on cladistic analysis of larvae discussed above was also noted to be a problem by Ashe in studies of relationships of adults. Ashe (1984) found that relationships of *Agaricochara* among gyrophaenine genera was uncertain and provided two hypotheses about relationships of this genus. Based on the shared apotypy of a divided ligula, he proposed that *Agaricochara* formed the basal lineage of the "*Sternotropa*" lineage. However, he noted that *Agaricochara* also shared a number of apotypic features with members of the "*Gyrophaena*" lineage. Therefore, based on these, he provided an alternative hypothesis in which *Agaricochara* formed the basal lineage of the "*Gyrophaena*" lineage. Because most of the apotypic states which supported this latter hypothesis were either reductions or likely to be subject to parallelisms (based on frequent parallel development of similar apotypic features in well-established lineages), he tentatively accepted the placement of *Agaricochara* in the "*Sternotropa*" lineage. He further noted that evidence for this hypothesis was weak and contradictory and that considerably more study of the relationships of *Agaricochara* among gyrophaenine genera was required.

Cladistic analyses of larval characteristics are enlightening but do not effectively solve the problem of relationships of *Agaricochara.* As with adult features, larvae of *Agaricochara* are relatively plesiotypic or have many character states intermediate between those of members of the "*Sternotropa*" and "*Gyrophaena*" lineages. Of the two hypotheses, Hypothesis I is similar to Ashe's tentatively accepted hypothesis of relationships of adult gyrophaenine genera in that it places *Agaricochara* as a basal member of the "*Sternotropa*" lineage. However, as noted above, this is supported by only a single shared apotypic character state. If, however, the small spinose sensilla on each side of the midline of the ligula of larvae of *Agaricochara* (fig. 4) is hypothesized to be homologous to the distinct setose sensilla in a similar position on larvae of *Brachychara* (fig. 34) and *Agaricomorpha* (fig. 19), the position of *Agarico-*

chara within this lineage becomes much more firmly supported.

The alternative hypothesis, Hypothesis II, which places *Agaricochara* as sister group of the "*Gyrophaena*" + "*Sternotropa*" lineage is also only very weakly supported (see discussion above). Furthermore, no presently reasonable reanalysis of characters provides additional support for this grouping of taxa.

The minimum length tree which is required to place *Agaricochara* as a basal lineage of the "*Gyrophaena*" lineage is 42. Therefore, this hypothesis of Ashe (1984) is not corroborated by cladistic analysis of larvae. This provides limited confirmation for Ashe's conclusion that most of the apotypic features which are shared by adults of *Agaricochara* with members of the "*Gyrophaena*" lineage are derived in parallel.

Another discrepancy between cladograms based on adult and larval features is in relationships among members of the "*Gyrophaena*" lineage. Ashe (1984) hypothesized that *Eumicrota* was the sister group to *Gyrophaena* + *Phanerota* based on three relatively weak shared apotypic states between the latter two taxa. No evidence for this series of relationships is provided by analysis of larval features, which consistently place *Phanerota* and *Eumicrota* as sister groups based on two shared apotypies. No resolution of this discrepancy is possible at this time.

It is also interesting that the monophyly of the genus *Gyrophaena* is not supported by cladograms based on either larvae or adults. However, *Eumicrota,* which cannot be demonstrated to be monophyletic based on available larval characters, can be hypothesized to be monophyletic based on strong autapotypic adult characteristics (Ashe, 1984).

Reanalysis of character states based on additional study of both adult and larval gyrophaenines would seem to be required.

Summary and Conclusions

This study represents the first comparative use of the system for naming setae and discussing variation in the chaetotaxic system of aleocharine larvae developed by Ashe and Watrous (1984). The variety of characteristics in chaetotaxic structure which proved to be useful at the generic level for systematic and phylogenetic study of gyrophaenine larvae is impressive. The system proved especially useful in this study because it is only when chaetotaxic features are studied comparatively among taxa that the wealth of structural variation and the taxonomic level of stability of various characteristics become apparent. Several general features of levels of stability in chaetotaxic characteristics among gyrophaenine larvae accent the information content of these structures. These include (1) uniformity of chaetotaxic features among species in a genus, (2) uniformity of chaetotaxic features among individuals within a species, (3) phylogenetic correlation of chaetotaxic characteristics with other phylogenetically informative structural features, and (4) uniformity of many chaetotaxic character states within a monophyletic lineage. Though the system of Ashe and Watrous (1984) may require modification with continued study of aleocharine larvae, it seems to provide an initial base which should considerably stimulate comparative study of systematics and phylogenetic relationships among aleocharine larvae.

This study also represents the first attempt to develop hypotheses about cladistic relationships among genera of aleocharines based on larval characteristics. As such, it provides an initial set of phylogenetically analyzed character systems which can form the basis for testing and developing character systems for other groups of aleocharine larvae. Especially important, it provides an unusual opportunity to test the hypotheses about cladistic relationships among gyrophaenine genera based on adult features developed by Ashe (1984). Since Ashe based many decisions about classification and evolution of gyrophaenines on these cladistic hypotheses, it subsequently provides an independent test of these decisions.

Eldredge (1979) correctly points out that a cladogram is testable by the addition of new data (such as characters) among taxa already analyzed. Cladistic study of larvae would appear to represent a nearly ideal test of cladistic hypotheses based on adults, since cladistic analysis of larvae is based on an entirely independent set of character systems. The analysis can therefore be done without inclusion of any of the information or biases which were used when developing initial hypotheses about relationships among genera.

The similarity between cladograms based on adult and larval features is striking. The number of correlated apotypic characteristics shared among all gyrophaenine larvae provides additional strong support for the hypothesis that the Gyrophaenina form a monophyletic group. In addition, monophyly of the "Gyrophaena" lineage (Ashe, 1984)

is given strong support by larval characters. Monophyly of this lineage was previously only supported by adult characters of uncertain reliability. Support for the monophyly of the "Sternotropa" lineage is also present but not as convincingly since larvae of many genera of this lineage are not available. However, monophyly of the lineage represented by *Agaricomorpha* + *Brachychara* is well corroborated by the two cladograms. In addition, apotypic features shared by larvae of these two genera but absent from those of *Agaricochara* further confirm the decision of Ashe (1984) to treat *Agaricomorpha* as a genus separate from *Agaricochara*.

The fact that larvae of *Agaricochara* do not have synapotypic features characteristic of members of the "Gyrophaena" lineage supports Ashe's conclusion that apotypic features shared by adult *Agaricochara* and members of this lineage are parallelisms. However, two equally probable placements of *Agaricochara* within the larval cladogram do not provide any additional insight into relationships of this relatively plesiotypic genus.

Discrepancies in hypothesized relationships among genera of the "Gyrophaena" lineage between larval and adult cladograms cannot be resolved at present. However, these differences do not seriously affect either the classification or the hypotheses of major evolutionary features of gyrophaenines proposed by Ashe (1984).

This level of correspondence between cladograms of genera based on independent sets of character systems and the variety of characters available for study is surprising, especially when one considers the great diversity, taxonomic difficulty, and initial impression of superficial similarity among taxa within the staphylinid subfamily Aleocharinae. It would seem to offer considerable hope that a phylogenetically meaningful and stable higher-level classification of this currently chaotic subfamily is an ultimate possibility. The character systems to do this are available on both larvae and adults.

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